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THE UNIVERSITY OF ALBERTA

A BIOSYSTEMATIC REVISION OF ARNICA L. (COMPOSITAE) SUBGENUS AUSTROMONTANA MAGUIRE

by

© STEVEN J. WOLF

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "A Biosystematic Revision of *Arnica* L. (Compositae) subgenus *Austromontana* Maguire" submitted by Steven J. Wolf in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

ABSTRACT

A morphological, cytological and phytochemical analysis resulted in a systematic revision of Arnica subgenus Austromontana. Nine species with no infraspecific or infrageneric taxa are recognized. The basic chromosome number of the subgenus, $x = 19$, has been confirmed; with A. cernua, A. viscosa and A. venosa having $2n = 38$; A. nevadensis $2n = 76$; A. gracilis $2n = 57$ and 76; and A. spathulata, A. latifolia and A. discoidea largely $2n = 38$ with a few populations of each having $2n = 76$. Arnica cordifolia, with six chromosome races, is recognized as a mature polyploid complex. Tetraploids ($2n = 76$) are widespread, with only a few widely scattered diploid ($2n = 38$) populations known, triploids ($2n = 57$) occur mainly in the front ranges of the Rocky Mountains, pentaploids ($2n = 95$) occur in Colorado and two hexaploid ($2n = 114$) populations are known. A total of 26 flavonoids, including 12 glycosides and 14 free aglycones; have been isolated and identified in 89 populations of the subgenus. The plants elaborate a wide range of compounds including common flavone and flavonol glycosides and more complex mono-, di- and tri-methyl flavones as well as a 6-hydroxy 4'-methyl flavone. Several compounds are present in all nine species (e.g., Viscosin and Quercetin Gentiobioside), some are restricted to a few or even only one species (e.g., Apigenin 7-0-glucoside and Luteolin 6OH, 4'methyl ether), certain compounds such as Luteolin 7-0-glucoside and its 6-methyl ether indicate phylo-

genetic relationships, the distribution of some compounds (e.g., Quercetin and Kaempferol 3-O-glucoside) appears to be random and other compounds have significant geographical correlations. The two widespread species, *A. cordifolia* and its early derivative, *A. latifolia* are ancestral species of the subgenus. From these two species, major evolutionary diversification within the subgenus has taken place largely in the Klamath region of Oregon and California, resulting in the formation of several rare, endemic species. This narrow endemism is generally accompanied by a depletion of the parental flavonoid profiles; however, one species, *A. viscosa*, a rare volcanic endemic, exhibits the most elaborate and specialized flavonoid profile within the subgenus. Flavonoid data also support a previously suggested hybrid origin for *A. gracilis*. The flavonoid profile of this species is essentially a summation of its presumed parents, *A. cordifolia* and *A. latifolia*.

A complete nomenclatural revision of the nine species of the subgenus resulted in the location of and correct determination of several type specimens as well as the discovery of the holotype of *A. spathulata* in the Greene Herbarium at Notre Dame University.

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INTRODUCTION

The genus Arnica (Compositae: Senecioneae) is a circumboreal, predominantely montane genus of about 32 species. It extends southward from boreal regions, where four major southern radii of distribution can be recognized: (1) eastern North America south to northern Florida, (2) western North America south to New Mexico and southern California, (3) from northern Europe south to Spain and (4) northeast Asia south through Japan (Figure 1). In numbers of species, the genus exhibits its maximum diversity in the western cordillera (sensu lato) of North America with 26 species confined to or centered in this region. In the only comprehensive, worldwide treatment of the genus, Maguire (1943) recognized five subgenera:

Andropurpurea Maguire (3 species), Arctica Maguire (7 species), Austromontana Maguire (13 species), Chamissonis Maguire (7 species) and Montana Maguire (2 species).

The subgenus Austromontana as circumscribed by Maguire (1943) is distinguished by its turbinate to campanulate heads; white, barbellate pappus and mainly by its relatively broad leaves (Figure 2). The subgenus is confined entirely to western North America in predominantely montane areas, from central Alaska through northern New Mexico and southern California. Based on the presence or absence of ray florets, Maguire (1943) recognized two sections within Austromontana, the Eulatifoliae Maguire and the Eradiatae Maguire, respectively. The former consists of predominantely wide-

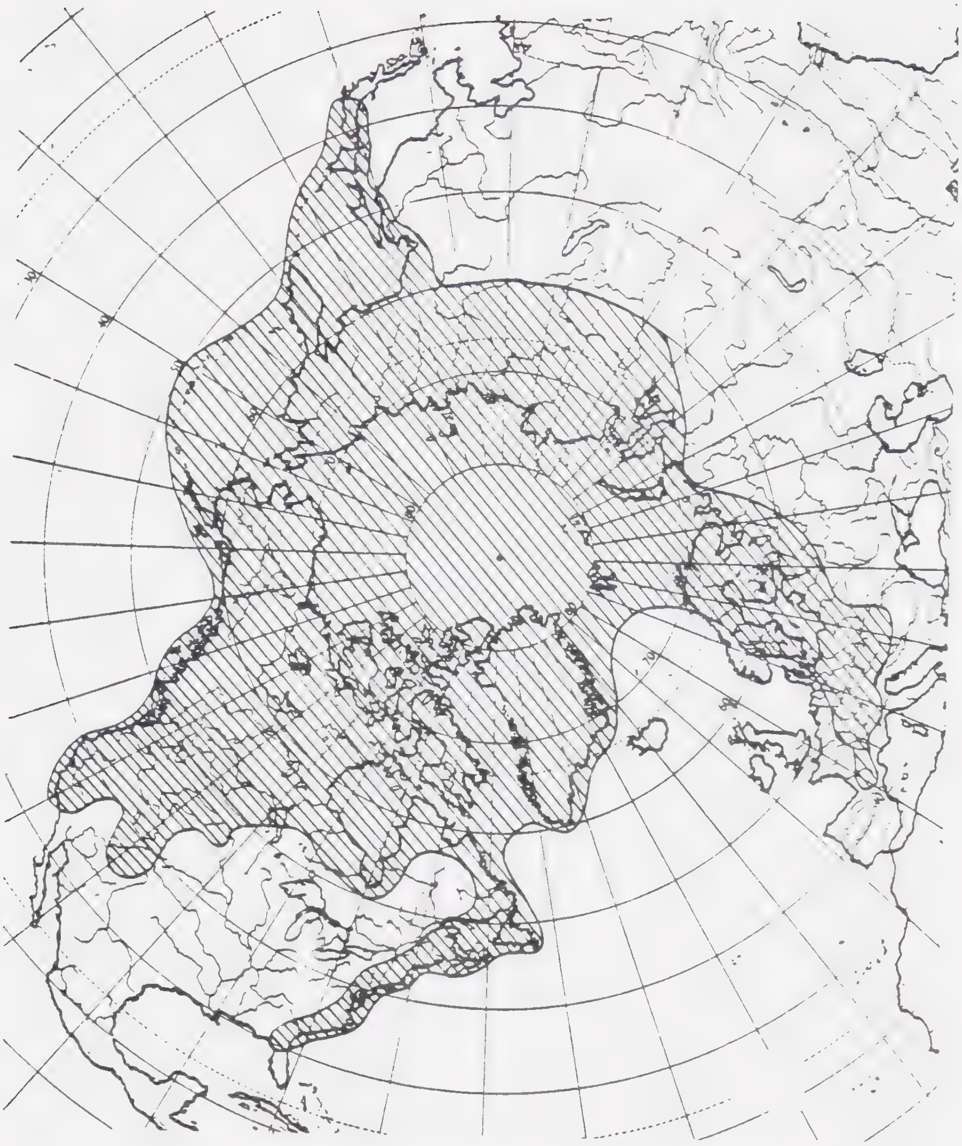
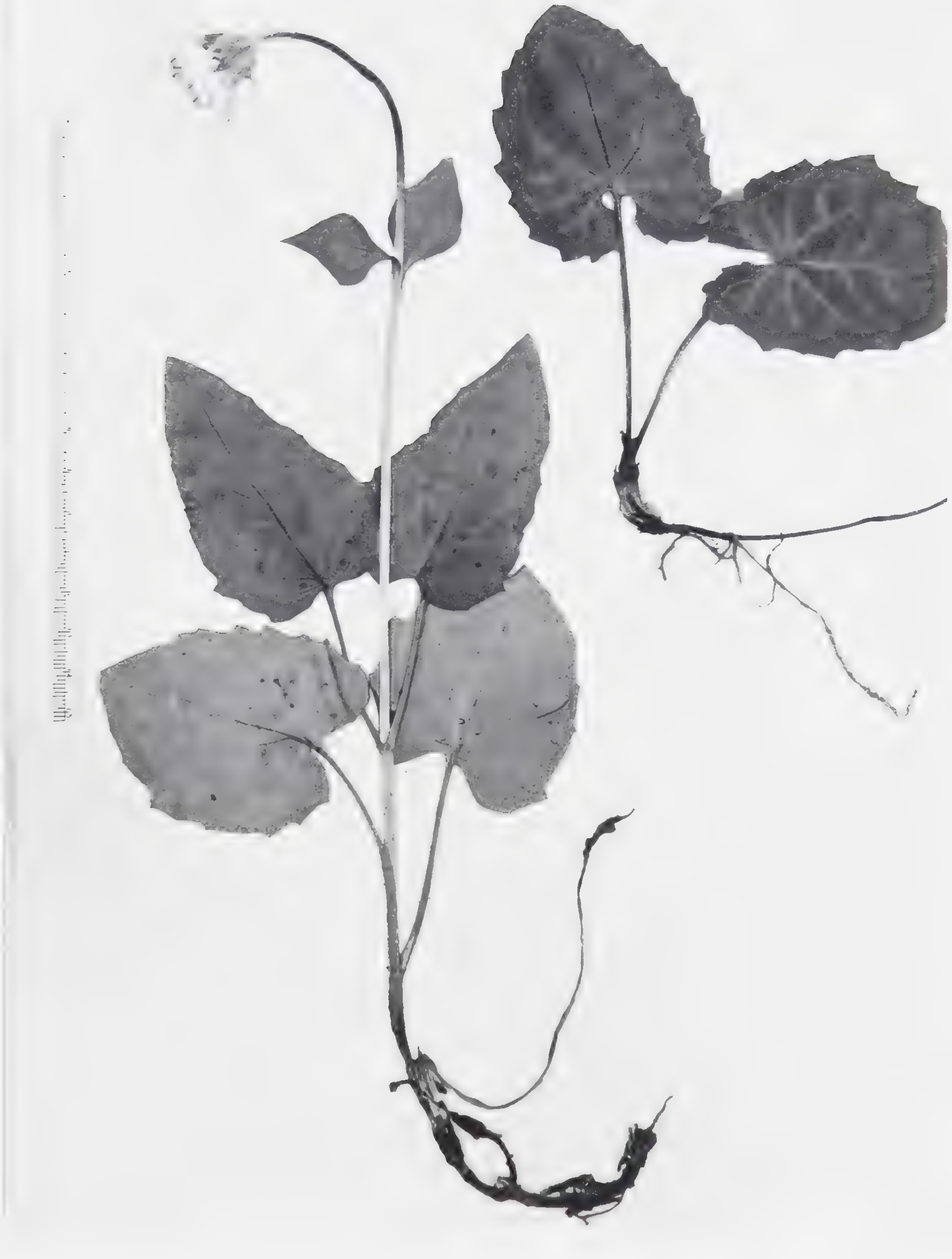


Figure 1. Worldwide distribution of the genus Arnica (Maguire, 1943).

Figure 2. *Arnica cordifolia*. A typical species of *Austromontana*.



ranging taxa while the latter is almost entirely confined to California and Oregon.

Maguire (1943) has provided an excellent historical account of the genus *Arnica*, consequently the following discussion will be largely confined to the subgenus *Austromontana*. According to Maguire (1943), the first appearance of the name *Arnica* in the literature was in 1625 and accompanied a woodcut of *A. montana* L. (referred to as *Caltha alpina*) in the herbal Kraüter-Buch of Theodorus Tabernaemontanus. After a long synonomy "...aber von den Medicis, *Arnica*" was added. The name *Arnica* next appeared in reference to *A. shroedri* (= *A. montana*) in Rupp's Flora Jenensis of 1718 (Maguire, 1943). In his *Flora Lapponica*, Linneaus (1737) recognized *A. montana* and *A. alpina* as *Doronicum foliis* oblongo-*ovalibus* and *D. foliislanceolatis*. By 1753, in his *Species Plantarum*, Linnaeus had adopted Rupp's name *Arnica* and recognized six species, only one of which (*A. montana*) has been retained within the genus. In 1788, Walter described the first North American *Arnica*, *A. acaulis* (Walt.) Britton (as *Doronicum acaule*) from "Carolina."

Bongard (1832) described the first species of the subgenus *Austromontana*, *A. latifolia* from Sitka, Alaska. Shortly thereafter, W.J. Hooker (1834) described *A. cordifolia*, the most widely distributed species of *Austromontana*. Hooker, in the same publication, also described *A. menziesii* which has subsequently been reduced to synonymy under *A. latifolia* (Herder, 1867). Nuttall

(1841) described *A. macrophylla* the first of many names to be subsequently reduced to synonymy under the highly polymorphic *A. cordifolia*. The first discoid species of the subgenus *Austromontana*, *A. discoidea* from Monterey, California, was described by Bentham (1849). In 1867, Herder recognized two varieties of *A. latifolia*, var. *genuina* and var. *angustifolia*.

In his *Synoptical Flora of North America*, Gray (1884) recognized fifteen species of *Arnica* and described three new species which were later included in the subgenus *Austromontana* by Maguire (1943). Of the three, *A. viscosa* and *A. nevadensis* are retained in the present investigation while *A. parviflora* is reduced to synonymy with *A. discoidea*. In the same publication, Gray described *A. discoidea* var. *eradiata* which was subsequently treated as synonymous with *A. grayi* by Maguire (1943), and as synonymous with *A. discoidea* in the present study.

From 1896 to 1927, in what later became *Austromontana*, literally dozens of new names were proposed by Nelson, Howell and the two "splitters of the west" (Radford *et al*., 1974) E.L. Green and P.A. Rydberg. Virtually all have since been placed in synonymy under one of the two highly polymorphic species *A. latifolia* or *A. cordifolia* (see Taxonomy chapter). Notable exceptions are *A. gracilis* Rydberg (1897) and *A. spathulata* Greene (1896), both of which are accepted as good species in the present study. Maguire (1943) also recognized *A. tomentella* proposed by Greene (1900) and *A. paniculata* described by Nelson (1909). In the present study the

former is treated as *A. nevadensis* while the latter is reduced under *A. cordifolia*. Of Howell's proposed names only *A. cernua*, a rare serpentine endemic of the Klamath Region of Oregon and California, is accepted in the present investigation.

In 1915, Hall described one of the rarest arnicas, *A. venosa* of Shasta Co., California. Gandoger (1918) proposed the name *A. eriopoda* which is here treated as synonymous with *A. latifolia*. Piper (1920) described two species, *A. andersonii* and *A. aphanactis* which have subsequently been reduced under *A. cordifolia* and *A. latifolia* respectively (Maguire, 1943).

A taxon of considerable phytogeographical interest, *A. whitneyi* of the Keewenaw Peninsula of Michigan, was described by Fernald (1935). Subsequently, it was treated as a disjunct subspecies of *A. cordifolia* by Maguire (1943) and later deprived of subspecific rank by Ediger and Barkley (1978). Results of the present investigation support Ediger and Barkley's treatment of this taxon.

In his monograph of *Arnica*, Maguire (1943) recognized 13 species and 6 subspecies in the subgenus *Austromontana* with 7 species and 2 subspecies in section *Eulatifoliae* and 6 species and 4 subspecies in section *Eradiatae* (Table 1). Maguire (1947) later recognized 4 varieties of *A. cordifolia* ssp. *genuina*: *cordifolia*, *macrophylla*, *pumila* and *humilis*. Cronquist (1955), in his treatment of *Arnica* for the *Flora of the Pacific Northwest*, included *A. grayi* and *A. paviflora* in the new combination *A.*

Table 1. The Species of *Arnica* Subgenus *Austromontana*

	Maguire (1943)		*Present Study*
	Sect. *Austromontana*		
1.	*A. cordifolia* Hook		
	subsp. *cordifolia*		
	subsp. *whitneyi* Maguire	1.	*A. cordifolia* Hook
2.	*A. paniculata* A. Nelson		
3.	*A. cernua* Howell	2.	*A. cernua* Howell
4.	*A. gracilis* Rydb.	3.	*A. gracilis* Rydb.
5.	*A. latifolia* Bong.	4.	*A. latifolia* Bong.
6.	*A. nevadensis* A. Gray		
		5.	*A. nevadensis* A. Gray
7.	*A. tomentella* Green		
	Sect. *Eradiatae* Maguire		
8.	*A. discoidea* Benth.		
9.	*A. grayi* A. Heller	6.	*A. discoidea* Benth.
10.	*A. parviflora* A. Gray		
11.	*A. spathulata* Greene		
	subsp. *spathulata*	7.	*A. spathulata* Greene
	subsp. *eastwoodiae* (Rydb.) Maguire		
12.	*A. venosa* H.M. Hall	8.	*A. venosa* H.M. Hall
13.	*A. viscosa* A. Gray	9.	*A. viscosa* A. Gray

discoidea var. eradiata (A. Gray) Cronquist and treated A. gracilis as a variety of A. latifolia. Shortly thereafter, Cronquist (1958) proposed the name A. discoidea var. alata (Rydb.) Cronquist for A. alata Rydb.

In their revision of Arnica for the North American Flora, Ediger and Barkley (1978) have essentially adopted Maguire's (1943) treatment of Austromontana, recognizing 9 species and treating his (Maquire's) subspecies as varieties. Exceptions include their acceptance of Cronquist's (1955, 1958) treatment of A. discoidea with 3 varieties (discoidea, alata and eradiata) and his recognition of A. gracilis as a variety of A. latifolia. In addition, Ediger and Barkley considered A. paniculata a possible hybrid between A. cordifolia and A. parryi A. Gray and therefore did not give it formal taxonomic recognition.

In a very recent systematic study, Straley (1980) recognized 7 species with no infraspecific taxa in a revised subgenus Austromontana and included A. venosa and A. viscosa in a new subgenus, Calarnica Straley.

Biosystematic studies within the genus Arnica have been confined largely to reports of chromosome numbers and investigations of reproductive behavior. Previously reported chromosome numbers in Austromontana are listed in Table 2. Battaglia (1955) proposed a basic chromosome number of $x = 5$ for the genus based on a count of $n = 5$ for A. longifolia from the botanical garden of the University of Copenhagen. However, upon re-examination of the material

Table 2. Previously reported chromosome numbers in *Arnica* subgenus *Austromontana* Mag.

Taxon	2n =	Locality	Reference
A. cernua	38	CA: Humboldt Co.	Straley (1980)
	38	CA: Humboldt Co.	Straley (1980)
	38	OR: Josephine Co.	Barker (1966)
A. cordifolia	38	MT: Missoula Co.	Schaack, *et al* (1974)
	60	Cult. USSR Bot. Gard.	Zhukova (1967)
	57	BC: Tod Mt.	Straley (1980)
	57	BC: Olalla	Straley (1980)
	57	BC: Kootenay Dist.	Straley (1980)
	57	BC: UBC Bot. Gard.	Straley (1980)
	57	BC: Windermere	Straley (1980)
	57	CA: Mono Co.	Straley (1980)
	57	CO: Grand Co.	Straley (1980)
	57	WY: Teton Co.	Straley (1980)
	72-76	OR: Lake Co.	Strother (1972)
	ca. 76	ID: Lewis Co.	Ornduff *et al* (1967)
	ca. 76	WA: Stevens Co.	Barker (1966)

76	ALT: Lake Louise	Straley (1980)
76	ALT: Moraine Lake	Straley (1980)
76	ALT: Peyto Lake	Straley (1980)
76	BC: Lambly Creek	Straley (1980)
76	BC: Botanie Valley	Straley (1980)
76	BC: Fountain Valley	Straley (1980)
76	BC: Bonanza Pass	Straley (1980)
76	BC: Hat Creek	Straley (1980)
76	BC: Sunday Summit	Straley (1980)
76	BC: Apex Mt.	Straley (1980)
76	BC: Kamloops	Straley (1980)
76	CA: Mono Co.	Straley (1980)
76	CA: Placer Co.	Straley (1980)
76	CA: Sierra Co.	Straley (1980)
76	CA: Siskiyou Co.	Straley (1980)
76	CO: Routt Co.	Straley (1980)
76	CO: Routt Co.	Straley (1980)
76	CO: Grand Co.	Straley (1980)
76	CO: Grand Co.	Straley (1980)
76	CO: Clear Creek Co.	Straley (1980)
76	CO: Boulder Co.	Straley (1980)
76	ID: Bonneville Co.	Straley (1980)

	76	MI: Keweenaw Co.	Straley (1980)
	76	MI: Keweenaw Co.	Straley (1980)
	76	MT: Missoula Co.	Straley (1980)
	76	OR: Wasco Co.	Straley (1980)
	76	SASK: Cypress Hills	Taylor & Brockman (1966)
	76	SD: Lawrence Co.	Straley (1980)
	76	WA: Okanogan Co.	Straley (1980)
	76	WA: Okanogan Co.	Straley (1980)
	76	WA: Klickitat Co.	Straley (1980)
	76	WA: Klickitat Co.	Straley (1980)
	76	YT: Rancheria	Straley (1980)
	ca. 90±6	CO: LaPlata Co.	Ornduff _et_ _al_ (1967)
	ca. 95±4	CO: Huerfano Co.	Ornduff _et_ _al_ (1967)
	ca. 95	CO: Larimer Co.	Ornduff _et_ _al_ (1967)
	114	ALT: Vermillion Pass	Straley (1980)
	114	WA: Okanogan Co.	Straley (1980)
A. discoidea	38	CA: Marin Co.	Straley (1980)
	38	CA: Mendocino Co.	Straley (1980)
	38	CA: Napa Co.	Straley (1980)
	38	CA: Santa Cruz Co.	Ornduff _et_ _al_ (1967)
	38	CA: Trinity Co.	Barker (1966)

	ca. 72-76	OR: Josephine Co.	Ornduff *et al* (1963)
	76	CA: Lake Co.	Ornduff *et al* (1963)
	76	CA: Orange Co.	Ornduff *et al* (1963)
	76	OR: Wasco Co.	Straley (1980)
	76	WA: Klickitat Co.	Straley (1980)
A. gracilis	57	ALT: Lake Louise	Straley (1980)
	57	ALT: Moraine Lake	Straley (1980)
	57	ALT: Peyto Lake	Straley (1980)
	57	BC: Monroe Lake	Straley (1980)
	57	BC: UBC Bot. Gard.	Straley (1980)
	ca. 76	ID: Valley Co.	Ornduff *et al* (1967)
A. latifolia	38	ALT: (no local)	Ornduff *et al* (1967)
	38	ALT: Grand Prairie	Straley (1980)
	38	ALT: Peyto Lake	Straley (1980)
	38	BC: Mt. Seymour	Straley (1980)
	38	BC: Vancouver Isl.	Straley (1980)
	38	BC: Bonanza Pass	Straley (1980)
	38	BC: Kootenay Pass	Straley (1980)
	38	BC: Manning Park	Straley (1980)
	38	BC: Nancy Greene P.P.	Straley (1980)

	38	BC: Black Tusk	Straley (1980)
	38	BC: Cypress Bowl	Straley (1980)
	38	BC: Queen Charlotte Isl.	Taylor & Mulligan (1968)
	38	BC: Queen Charlotte Isl.	Taylor & Mulligan (1968)
	38	MT: Missoula Co.	Straley (1980)
	38	MT: Ravalli Co.	Schaack *et al* (1974)
	38	WA: Chelan Co.	Straley (1980)
	38	WA: Chelan Co.	Straley (1980)
	38	WA: Kittitas Co.	Ornduff *et al* (1963)
	38	WA: Lewis Co.	Barker (1966)
	38	WA: Whatcom Co.	Ornduff *et al* (1963)
	38	WA: Whatcom Co.	Straley (1980)
	ca. 76	MT: Lake Co.	Powell *et al* (1974)
A. nevadensis	76	CA: Mono Co.	Straley (1980)
	76	CA: Sierra Co.	Straley (1980)
	76	NV: Washoe Co.	Straley (1980)
A. spathulata	38	CA: Del Norte Co.	Straley (1980)
	38	CA: Del Norte Co.	Straley (1980)
	38	CA: Del Norte Co.	Straley (1980)
	38	CA: Del Norte Co.	Ornduff *et al* (1967)

	38	OR: Josephine Co.	Straley (1980)
	38	OR: Josephine Co.	Straley (1980)
	38	OR: Josephine Co.	Straley (1980)
	38	OR: Josephine Co.	Straley (1980)
	38	OR: Josephine Co.	Straley (1980)
	ca. 76	OR: Josephine Co.	Barker (1966)
A. venosa	38	CA: Shasta Co.	Barker (1966)
	38	CA: Shasta Co.	Straley (1980)
	38	CA: Shasta Co.	Straley (1980)
	38	CA: Shasta Co.	Straley (1980)
A. viscosa	38	CA: Siskiyou Co.	Barker (1966)
	38	CA: Siskiyou Co.	Straley (1980)
	38	CA: Trinity Co.	Strother (1972)
	38	OR: Klamath Co.	Straley (1980)

available to Battaglia and several other Arnica species, Ornduff et al. (1967) concluded that the base number of the genus is, as suggested by Böcher and Larsen (1955), $\underline{x} = 19$.

Cytologically the genus is very diverse, with all ploidy levels from diploid ($2\underline{n} = 38$) through octoploid ($2\underline{n} = 152$) being reported (Ornduff et al., 1963, 1967; Moore, 1973, 1977; Keil and Pinkava, 1976). Previously, the genus had proven to be difficult to work with cytologically (Barker, 1966) and several chromosome counts have been reported which do not conform to the basic number of $\underline{x} = 19$ (cf. Fedorov, 1969). This has led to the suggestions of Ornduff et al. (1967) and Keil and Pinkava (1976) that counts based on radically different base numbers need to be reinvestigated or at least treated as approximations. Prior to 1966, of the 50 Arnica chromosome counts reported in the literature, 20 have been listed as approximations and 10 others are questionable (Barker, 1966). This situation is still evident in the present literature (cf. Moore, 1977). The difficulties encountered in obtaining accurate counts in the genus are not surprising, and few counts (other than diploids) have been reported without the authors noting a wide assortment of meiotic irregularities such as: a number of univalents, trivalents, chains, equational chromosome divisions, bridges and lagging chromosomes (Ornduff et al., 1967).

As early as 1936, Afzelius reported apomixis in three species of Arnica. Cronquist (1955) suggested that much of the perplexing morphological variability within the genus may be due to the exis-

tence of apomixis associated with polyploidy. Ornduff _et al._ (1963, 1967) suggested that meiotic irregularities observed in many _Arnica_ species are probably the result of apomixis. With these ideas in mind, Barker (1966) conducted a survey of the reproductive behavior of 24 species within the genus. Among his findings the following are relevant to the present investigation: (1) the diploid level indicates amphimixis and the polyploid level indicates apomixis, particularly if meiotic irregularities are observed; (2) virtually no diploid species occur in a glaciated area and no polyploid species occur in an unglaciated area; (3) some previously widespread diploid taxa survived in unglaciated areas and suffered biotype depletion, and these populations then gave rise to polyploid apomicts from which virtually all post-glacial colonization has taken place. The sexual populations are now virtually extinct, having made very little post-glacial recovery.

Barker's (1966) investigation has contributed greatly to an understanding of the relationships between polyploidy, apomixis and historical phytogeography in the genus _Arnica_. However, because of the wide scope of his study and the limited availability of material, he could only provide a somewhat cursory overview of the subject. Chromosome counts were not available for all the taxa investigated, sample sizes were quite small and no original locality data was available for material obtained from botanical gardens. In addition, Barker (1966) found _Austomontana_ to be taxonomically the most difficult and "...less amenable to investigation than

those [species] of other subgenera." Therefore, few specific conclusions about it could be made.

In a recent systematic study, Straley (1980) provided a further amplification of Barker's (1966) work on the breeding systems of *Austromontana sensu lato*. Although Straley had greater success than Barker in his experimental crosses, complicating factors such as polyploidy, apomixis and non-synchronous flowering periods caused the results to be fragmentary and incomplete (Figure 3). Such key crosses as *A. cordifolia* with *A. gracilis*, *A. nevadensis* and *A. discoidea*; and *A. spathulata* with *A. venosa* and *A. discoidea* could not be attempted. In addition, due to cultural problems no crosses at all could be made with *A. cernua*. Ultimately, Straley's deductions concerning evolutionary relationships were based, like those of Maguire (1943), on morphological features. Straley's (1980) proposed phylogeny of the subgenus *Austomontana sensu lato* is presented in Figure 4.

Very little is known about the flavonoid chemistry of the genus *Arnica*. Saner and Leupin (1966) found Kaempferol 3-monoglucoside, Quercetin 3-monoglucoside and Quercetin 3-glucogalacturonide in *A. montana* L. Borkowski *et al.* (1966) investigated the flavonoid chemistry of four species: *A. chammissonis* Less., *A. sachalinensis* (Regl.) A. Gray, *A. montana* L. and *A. whitneyi* Fern. (= *A. cordifolia*) and reported all contained astragalin, isoquercitrin, luteolin and luteolin 7-monoglucoside.

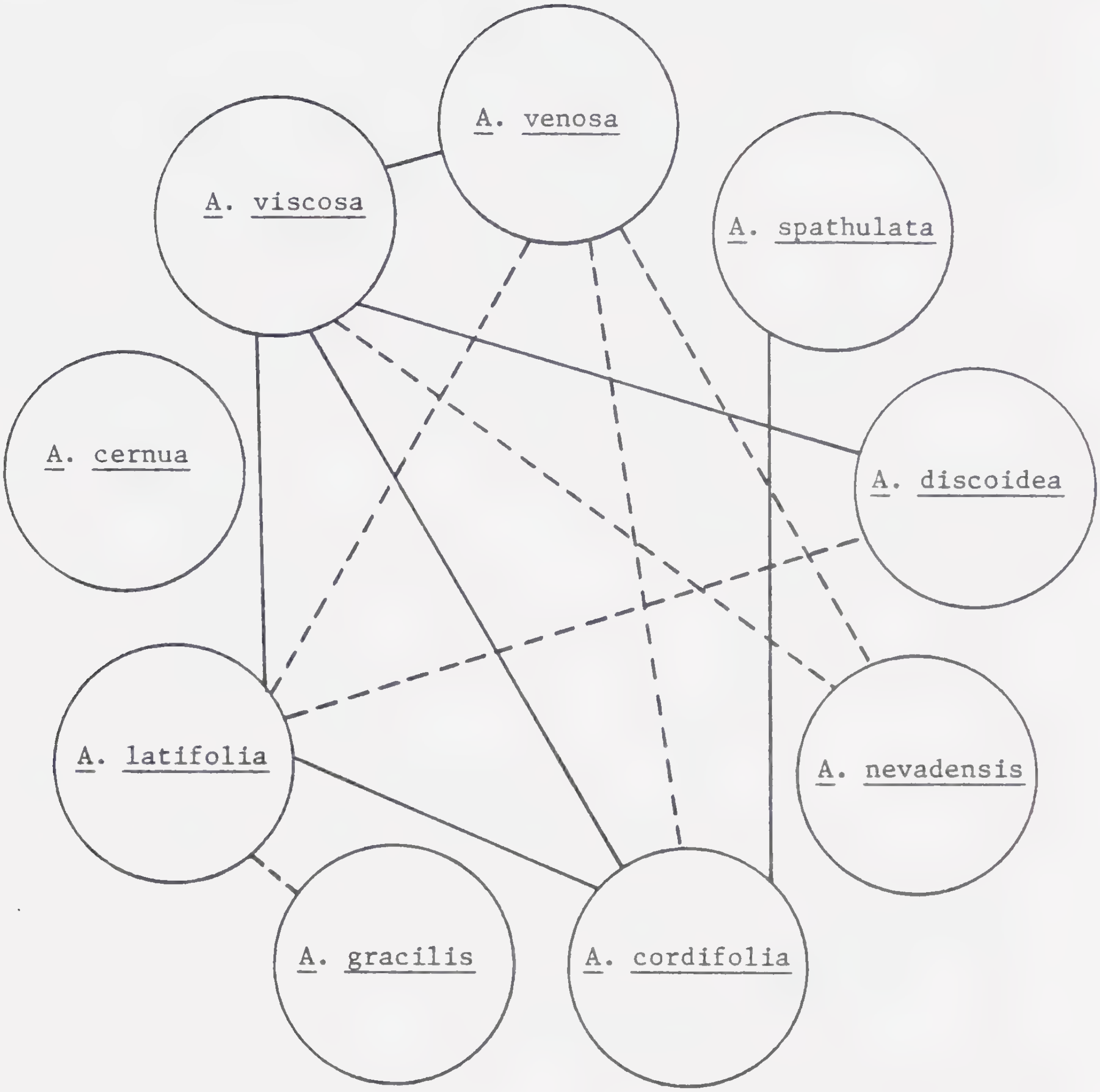


Figure 3. Summary of artificial crosses between the species of *Arnica* subgenus *Austromontana*. Solid lines indicate successful crosses. Dotted lines indicate unsuccessful crosses (Straley, 1980).

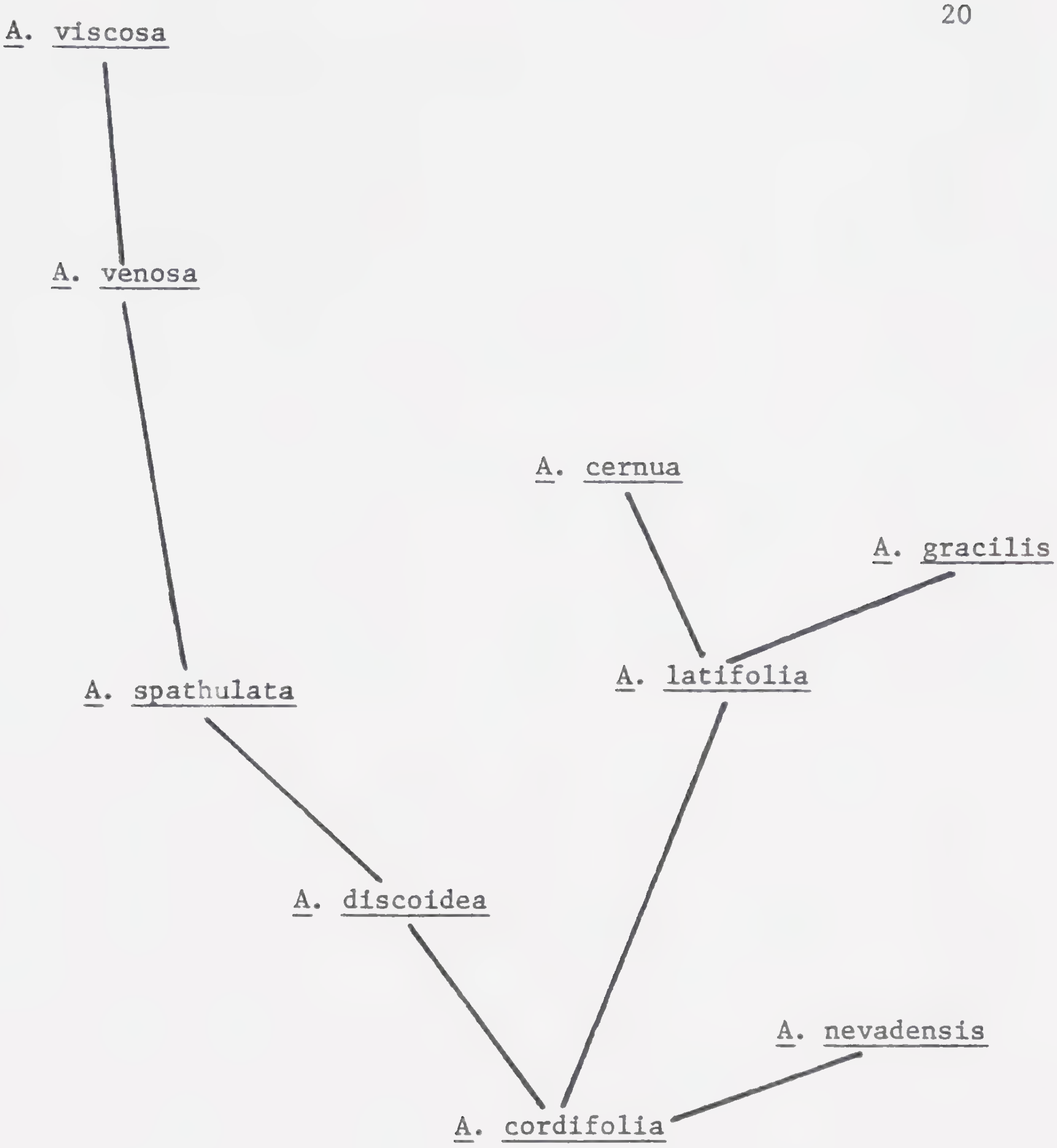


Figure 4 . Straley's (1980) proposed phylogenetic relationships of the species of Arnica subgenus Austromontana.

The subgenus Austromontana was chosen for the present investigation for several reasons. Barker (1966) found this taxon to be taxonomically the most difficult within the genus and therefore few concrete conclusions could be made about it. Also of prime consideration is the fact that Austromontana is the only major taxon within the genus that is totally accessable for collecting. Barker's general conclusions about apomixis, polyploidy and historical phytogeography within the genus Arnica suggested that further biosystematic investigations of Austromontana might prove useful in solving taxonomic problems and elucidating evolutionary relationships.

Grant (1971) has noted the importance of apomixis in plant speciation. Because apomictic populations are genetically isolated, they form numerous reproductively isolated micro-species which, over a period of time, can gradually evolve into new species. Also, according to Grant (1971), most apomictic taxa are derived via hybridization between different taxa. The implications of apomixis in Austromontana are twofold, in such wide ranging species as A. latifolia and A. cordifolia one might expect to find a great deal of variability due to both microspecies formation and hybridization. This may account for the large number of names proposed for these two taxa.

The most intriguing and relevant (to the present study) conclusion of Barker's (1966) work concerns the correlation of apomixis and polyploidy with glaciation. He states that "...no well-

developed [diploid] sexual species [of Arnica] occurs in a glaciated area, and no well-developed apomictic [polyploid] element occurs in an unglaciated area." He hypothesized that small sexual diploid populations survived in unglaciated areas and suffered biotype depletion and that apomixis bridged the self-incompatability barrier within the genus allowing recolonizaton of the glaciated areas. According to Barker (1966) the sexual diploid populations have made very little post-glacial recovery and are now very restricted or extinct.

With the advent of more sophisticated chromatographic techniques and a better understanding of the biosynthesis of flavonoids, these chemical compounds have been used extensively to detect hybridization (Smith and Levin, 1963; Alston and Turner, 1963), support taxonomic discriminations (Bierner, 1973; Crawford, 1973), suggest phyletic relationships (Stebbins *et al.*, 1963) and to demonstrate the influence of polyploidy on secondary metabolites (Levy and Levin, 1974, 1975). A systematic survey of the flavonoids of *Austromontana* could provide a great deal of taxonomic and evolutionary information of value in understanding and clarifying taxonomic relationships.

A major question within the subgenus is the relationship of the two sections *Eradiatae* and *Austromontana*. The former appears to be composed of several endemic discoid species related to much wider ranging radiate counterparts in the latter. In addition, *A. cordifolia* provides a unique opportunity to study the relationship

of polyploidy to flavonoid chemistry. Within this single species are found five chromosome races ranging from $2n = 38$ to $2n = 114$ (Ornduff *et* al., 1967; Straley, 1980).

Also of prime consideration in the present investigation is the relationship between flavonoid chemistry and geographical distribution. Denford (1973) has suggested that biochemical markers might be of use in establishing the existence of glacial refugia. Glennie *et al*. (1971) found significant correlations between flavonoid chemistry and plant geography in the *Senecio radican* complex. Turner (1972) suggested that chemosystematic data may be useful in the analysis of disjuncts. The disjunct populations of *A*. *cordifolia* pose interesting phytogeographical questions to which chemical investigations should be applied. The subgenus *Austromontana* contains several rare endemic taxa which should prove amenable to chemical analysis. Stebbins (1980) noted that rare species are often genetically depauperate, consequently it would be of interest to see if the flavonoid profiles of such rare species are also depauperate.

The recognition and investigation of endemic taxa is not only of scientific interest but also has practical applications for the conservation of rare and endangered species. Three taxa within *Austromontana*: *A*. *viscosa*, *A*. *venosa* and *A*. *whitneyi* (= *A*. *cordifolia*) have appeared on several state, provincial and national registers of rare and endangered species (Mosquin and Suchal, 1977; Ayensu and DeFilipps, 1978; Smith *et al.*, 1980). An evaluation of

their status is of prime interest in the present investigation.

Rollins (1972), in stressing the need for care in choosing lectotypes, noted "...the holotype is the particular specimen retained by the original author at his place of work or in his private herbarium..." He further stated, "the existence of a holotype in the institution where the original author worked is assumed until proved otherwise." Several typification errors in _Austromontana_ have resulted in the past from failure to consult authors' private herbaria. In the present study an effort was made to locate all type specimens and to examine the herbaria of all authors who published names in _Austomontana_. This was especially critical for the specimens of E.L. Greene who worked at several institutions and published about 20 names within the subgenus.

The present study was initiated to provide a biosystematic revision of _Arnica_ subgenus _Austromontana_ using morphological, cytological, chemical and phytogeographical data in an effort to elucidate: (1) the taxonomy and nomenclature of the subgenus, (2) the role of polyploidy in the evolution of the subgenus and its effect on flavonoid chemistry, (3) possible relationships between distribution and historical factors and, (4) the phylogenetic relationsips between the several species.

MATERIALS AND METHODS

Collections

Field collections of taxa within *Arnica* subgenus *Austromontana* were made throughout virtually the entire range of the taxa. Material of eastern disjunct populations of *A. cordifolia* was supplied by the Michigan Nature Association and Dr. G.B. Straley. Collections from each locality included, where possible, pressed specimens, a quantity of air dried, unpressed material for use in chemical studies, mature achenes and immature capitula for chromosome studies. In addition, live plants were transplanted into 10 cm pots and brought back to the greenhouse facilities of the University of Alberta.

Herbarium Studies

Structural and distributional studies were based on living material and over 13,000 herbarium specimens from the following herbaria: University of Alaska (ALA); University of Alberta (ALTA); British Museum (BM); Brigham Young Universty (BRY); National Museum of Canada, Ottawa (CAN); California Academy of Sciences (CAS); Crater Lake National Park (here designated CLNP); Department of Argriculture, Ottawa (DAO); Dudley Herbarium of Stanford University (DS); Gray Herbarium of Harvard University (GH); Humboldt State University (HSC); Jepson Herbarium, University of California (JEPS); Royal Botanic Garden, Kew (K); Catholic

University of America (LCU); Komarov Botanical Institute, Leningrad (LE); University of Michigan (MICH); Missouri Botanical Garden (MO); Montana State University (MONT); University of Notre Dame (ND); Greene Herbarium, University of Notre Dame (NDG); New York Botanical Garden (NY); University of Oregon (ORE); Oregon State University (OSC); Pomona College (POM); Pacific Union College (PUA); University of Nevada, Reno (RENO); Rocky Mountain Herbarium, University of Wyoming (RM); Rancho Santa Ana Botanical Garden (RSA); Shasta-Trinity National Forest (here designated STNF); University of British Columbia (UBC); University of California, Berkeley (UC); University of California, Santa Barbara (UCSB); U.S. National Herbarium (US); Intermountain Herbarium, Utah State University (UTC); University of Wisconsin (WISC); Washington State University (WS) and University of Washington (WTU).

Chromosome Counts

Immature capitula were fixed in the field in modified Carnoy's fixative (4 chloroform: 3 ethanol: 1 glacial acetic acid) and floret buds were stained with iron-acetocarmine. Mitotic counts were obtained from root tips of plants transplanted from the field and field seed collections. Achenes from disc florets were placed in water for 24 hr, the exocarp removed and germinated at 20°C under a 16 hr photoperiod (G. Straley, personal communication). Root tips were pretreated in water saturated p-dichlorobenzene for 3 hr at 4°C (Sharma and Sharma, 1965), fixed in Carnoy's (4:3:1),

hydrolyzed in HCl-Ethanol (1:1) at 20°C for 2 min and stained in aceto-orcein for 30 min. Voucher specimens are deposited at the Herbarium of the University of Alberta (ALTA).

Flavonoid Chemistry

Identification of the leaf flavonoids of 26 populations was carried out. In addition to the identification of compounds in these 26 populations, chromatographic profiles of 73 populations were compared. The populations were carefully chosen to insure representation of all geographic areas and ploidy levels within the subgenus *Austromontana*.

Extraction of flavonoids was carried out using slightly modified procedures of Neuman, Timmerman and Mabry (1979). Prior to chemical analysis the plants to be used were sorted to remove any contaminants. Twenty to 80 gm (dry weight) of plant material was ground to powder in a blender and extracted for 24 hr on a shaker, twice with 1ℓ of 85% methanol and once with 1ℓ of 50% methanol. Fractions were combined, filtered and reduced *in vacuo* to 20-30 ml. Chlorophylls and flavonoid aglycones were removed by partitioning the aqueous extract 6X with a 4 volume excess of hexane followed by a 6 volume excess of chloroform until no green color remained in the final chloroform layer. Subsequent analysis indicated that the aglycones in the hexane and chloroform extracts were the same and therefore the extracts were combined (Roberts, Timmerman and Mabry; 1980). This combined fraction will hereafter be referred to as the

hexane fraction. Neuman et al. (1979) suggest further partitioning of the remaining aqueous fraction with ethyl acetate to separate monoglycosides from di and triglycosides. This procedure was used several times but subsequently abandoned because it failed to yield definitive separation.

Preliminary analysis of the hexane and aqueous fractions was carried out on Whatman 3 MM chromatography paper using standard 2-dimensional chromatographic procedures in BAW (n-butanol-acetic acid-water, 4:1:5 upper phase) and 15% acetic acid (Mabry, Markham and Thomas; 1969). In addition, in order to facilitate aglycone separation, the second dimension of the hexane chromatograms was run for 4-6 times the normal time, i.e. 24-36 hr, with the lower edge serrated.

Isolation of aglycones in the hexane fractions was carried out using two procedures. Extracts which contained a large number of aglycones (*A. viscosa* and *A. gracilis*) were chromatographed over a 5.5 x 60 cm column of Polyclar AT polyamide (GAF Corp) packed in the elution solvent. The column was first eluted in chloroform: methanol (9:1) and monitored using a UV lamp. When the flavonoid bands stopped moving, the polarity of the solvent was increased by increasing the proportion of methanol. Fractions off the column were reduced under pressure and purified by streaking on Whatman 3 MM paper in 15% acetic acid for 36 hr with the lower edge of the paper serrated. For all other populations the column procedure was eliminated and the hexane fractions were streaked directly on 3 MM

paper in 15% acetic acid for 36 hr. Final purification of all aglycones was carried out on small columns of Sephadex LH-20 in methanol. Mass spectra were obtained for several of the underivatized aglycones (Mabry and Markham, 1975).

Flavonoid glycosides present in the aqueous fraction were isolated on a 5.5 x 60 cm column packed with Sephadex LH-20 and eluted in methanol. Fractions off the column were reduced under pressure and purified by streaking on Whatman 3 MM paper in either 15% acetic acid or water.

The isolated flavonoids were identified using standard chromatographic, hydrolytic and spectral procedures. Rf's were determined on Whatman 1 MM paper using descending chromatography in four solvent systems: BAW, 15% acetic acid, water and saturated phenol (phenol-water, 4:1). Approximately 2 μℓ of a 10^{-3} M solution of Rutin (Quercetin 3-O-rutinoside) was spotted on each sheet to serve as a reference.

Ultraviolet spectral analysis using a Unicam SP 1800 spectrophotometer was carried out on each unknown using the procedures of Mabry _et al._ (1969). These procedures include the comparison of methanol scans with those obtained after the addition of several diagnostic agents. Solutions used included sodium methoxide, aluminum trichloride, aluminum trichloride plus hydrochloric acid, sodium acetate and sodium acetate plus boric acid.

Aglycones of the unknowns were separated by ether extraction after hydrolysis of methanolic solutions with an equal amount of

10% HCl at 100°C for 3-60 min. The ether fraction was evaporated to dryness, redissolved in a minimum volume of methanol and co-chromatographed with known standards on Whatman 1 MM paper in BAW, 15% acetic acid and saturated phenol. The aglycones were also subjected to standard UV spectral procedures.

The flavonoid glycosidic sugars, which remained in the acidic aqueous fraction after ether partitioning, were identified by chromatography with standards on silica gel plates (DC-Fertigplatten Sil G-25). The plates were run twice in ethyl acetate-isopropanol-water (65:22:11), air dried, sprayed with a mixture of 85% phosphoric acid-acetic acid-aniline-diphenylamine (20 ml:100ml:5ml:5gm) and developed by heating at 100°C for 2-3 hr.

After the identification of the compounds of the 26 populations was completed, a chromatographic analysis of the spot patterns of the 73 populations was conducted. Populations used in flavonoid analysis are listed in Table 3. Ten to 20 gm dry weight of material was extracted with 500 ml, 85% methanol for 12 hr on a shaker. The extracts were reduced to a volume of 20ml and chromatogrammed using standard 2-dimensional procedures. To facilitate aglycone detection the second dimension of additional sheets were run in 15% acetic acid for 36 hr with the lower edge serrated. Spot patterns, color reactions in NH_3 and after spraying with Diphenylboric acid (NA) in methanol were then compared with those of the master chromatograms from populations in which compounds were identified.

Table 3. Populations of *Arnica* subgenus *Austromontana* used in flavonoid analysis.

Species	2n =	Collection #	Location
A. cernua	38	W471*	CA: Humboldt Co.
	38	W464*	OR: Josephine Co.
A. cordifolia	57	F77122	ALT: Crows Nest Pass
	57	F77102	ALT: Kananaskis Forest
	76	F77104	ALT: Nordegg
	76	E7801	ALT: Mayberne
	76	W308	ALT: Kananaskis Forest
	76	D7846	ALT: Maligne Lake
	76	F77134	ALT: Mt. Park
	?	B80052*	BC: Savona
	38	W306	BC: Haines Rd.
	76	W304	BC: Carcross Rd.
	76	B80060	BC: Clinton
	76	B80055	BC: Osoyoos
	76	W441	BC: Cranbrook
	76	W476	CA: Nevada Co.
	76	W413	CO: Summit Co.
	95	W399	CO: Pitkin Co.
	38	W347*	ID: Lewis Co.
	76	W354*	ID: Idaho Co.
	57	W496	MT: Flathead Co.

	76	W435	MT: Deerlodge Co.
	76	W480	NV: White Pine Co.
	?	S1849	ONT: Sibley P.P.
	38	W447*	OR: Wallowa Co.
	76	W448	OR: Wallowa Co.
	76	W398	UT: Duchesne Co.
	76	W481	UT: Iron Co.
	76	W368	WA: Chelan Co.
	76	W446	WA: Asotin Co.
	57	W430	WY: Teton Co.
	38	W505*	YT: Canol Rd.
	38	W507*	YT: Canol Rd.
	57	W499	YT: Carcross
	76	W498	YT: Carcross
A. discoidea	38	W470*	CA: Trinity Co.
	38	W390	CA: Trinity Co.
	38	W389	CA: Humboldt Co.
	38	W466	CA: Siskiyou Co.
	38	W472	CA: Humboldt Co.
	38	W475*	CA: San Mateo Co.
	38	W474*	CA: Mendocino Co.
	57	W477	CA: Plumas Co.
	76	W392	CA: Plumas Co.
	76	W473	CA: Lake Co.
	?	W515	CA: Santa Barbara Co.

A. gracilis	76	W324*	ALT: Kananaskis Forest
	76	W350*	ID: Idaho Co.
A. latifolia	38	W503	AK: Hatcher Pass
	38	W321	ALT: Kananaskis Forest
	38	W319	ALT: Kananaskis Forest
	38	W513*	ALT: Banff Park
	76	D7830	ALT: Waterton Park
	76	W465	CA: Siskiyou Co.
	76	W467	CA: Siskiyou Co.
	38	W416	CO: Clear Creek Co.
	38	W357	ID: Valley Co.
	38	W352	ID: Idaho Co.
	76	W490	ID: Idaho Co.
	76	W360	ID: Valley Co.
	76	W488*	ID: Lemhi Co.
	38	W344	MT: Lincoln Co.
	76	W494	MT: Flathead Co.
	76	W489	MT: Flathead Co.
	76	W436	MT: Deerlodge Co.
	38	W380	OR: Clackamas Co.
	38	W379	OR: Clatsop Co.
	38	W457	OR: Curry Co.
	38	W397*	UT: Duchesne Co.
	38	W376	WA: Pierce Co.
	38	W372	WA: Challam Co.

	38	W369*	WA: Okanogan Co.
	38	W424	WY: Albany Co.
	38	W431	WY: Teton Co.
A. nevadensis	76	W381*	OR: Klamath Co.
	76	W382	OR: Klamath Co.
A. spathulata	38	W458*	CA: Del Norte Co.
	76	W459*	CA: Del Norte Co.
	38	W455*	OR: Josephine Co.
	38	W456*	OR: Josephine Co.
	38	W462*	OR: Josephine Co.
	38	W463*	OR: Josephine Co.
	38	W384	OR: Josephine Co.
	38	W460	OR: Josephine Co.
	76	W461	OR: Josephine Co.
A. venosa	38	W468*	CA: Shasta Co.
	38	W469	CA: Shasta Co.
A. viscosa	38	W391*	CA: Siskiyou Co.
	38	W511	OR: Klamath Co.

*Populations used for full flavonoid characterization. Remaining populations were analyzed by 2-dimensional chromatography only.

MORPHOLOGY

In the present study, nine species with no infraspecific taxa are recognized in the subgenus Austromontana (Table 1, page 8). No new taxa are proposed; however, several taxa previously recognized by Maguire (1943) are placed in synonymy with these nine species.

In a discussion of the morphology of the genus Arnica, Maguire (1943) noted that there are some sharply defined species and a large number of other loosely-knit polymorphic ones. Within subgenus Austromontana most taxa fit into the latter category. Only A. cernua, A. viscosa and to some extent A. venosa are morphologically well defined. The remaining six species are highly polymorphic and show a wide range of morphological intergradation. In addition, superimposed upon this interspecific variability is a great deal of intraspecific variability. Indeed, Gustafsson (1947) and later Cronquist (1955) suggested that apomixis and polyploidy are probably largely responsible for the perplexing morphological variability within the genus. That A. venosa, A. viscosa and A. cernua are the only well defined species in Austromontana is not surprising since Straley (1980) has shown them to be the only entirely sexual, diploid taxa in subgenus Austromontana. Maguire (1943) has discussed the effect of environmental factors on the morphology of several species. Further discussion and specific examples are provided, where appropriate, in the Taxonomy section.

Although the several species of subgenus *Austromontana* are highly variable, a combination of several morphological features in conjunction with ecological and distributional data are sufficient to distinguish among them. Comparative morphological characters of the nine species subgenus *Austromontana* are presented in Table 4.

The following discussion will deal with some aspects of the morphology, otherwise detailed in the species descriptions. I will try to stress evolutionary trends in order to establish plesiomorphous and apomorphous conditions in the characters discussed. This will form the foundation for the phylogenetic discussion to be presented elsewhere.

Maguire (1943) has discussed several major evolutionary trends within the genus *Arnica*. Characters considered plesiomorphous by him include: broad, hemispheric, solitary, radiate heads with a white, barbellate pappus and simple, unbranched stems with leaves generally below the middle. In contrast, narrowly turbinate, numerous, discoid heads with a tawny, plumose pappus and highly branched, leafy stem are considered apomorphous (his reasons are presented in the Phylogeny section). Indeed, Cronquist (1977) considers few heads and the radiate condition to be a plesiomorphous condition within the Compositae in general. In the present study, Maguire's observations on evolutionary trends within the genus *Arnica* in general have been confirmed for the subgenus *Austromontana*. In the following discussion of morphological characters deemed taxonomically significant, suggestions of evolution-

Table 4. Comparative morphological characters of the nine species of *Arnica* subgn. *Austromontana*.

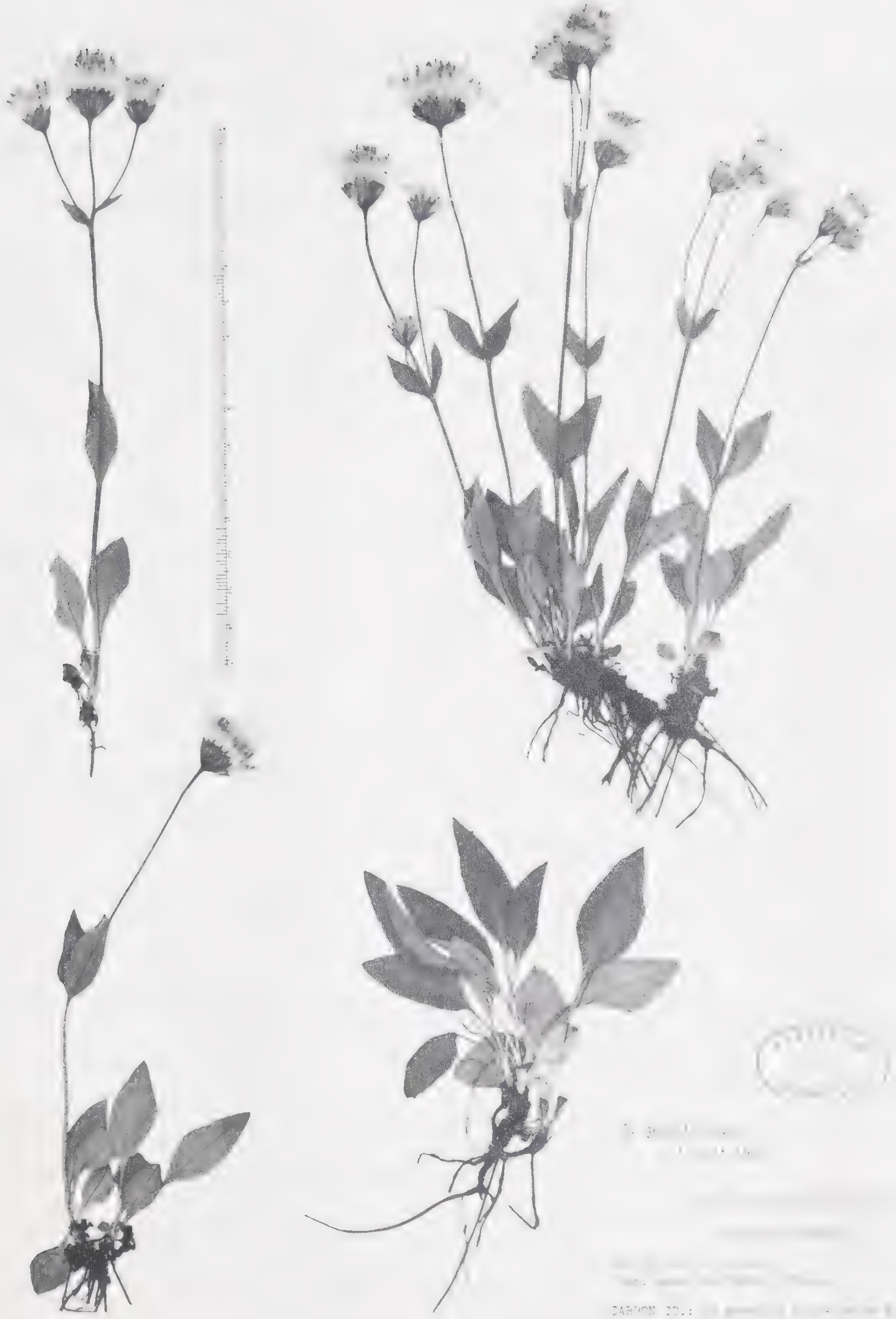
	A. cordifolia	*A. cernua*	*A. discoidea*	*A. gracilis*	*A. latifolia*	*A. nevadensis*	*A. spathulata*	*A. venosa*	*A. viscosa*
Stem branching	-	-	+-	+	-(+)	-	+-	+-	++
Underground parts	rhizome	rhizome	rhizome	rhizome	rhizome	rhizome	rhizome	woody caudex	woody caudex
Innovations	+	+	+	+	+	+	+	-	-
Leaves: # pair	2-4	2-3	3-7	2-3	2-4	2-3	3-5	6-10	numerous
shape	cordate	elliptic to ovate	ovate to brd. lanceolate	ovate-lanceolate	ovate	ovate to elliptic	spathulate	ovate to elliptic	ovate-oblong
margin	dentate	crenate	serrate to dentate	serrate	serrate to dentate	entire	dentate	coarsely serrate	entire
pubescence	±villous ±glandular	glabrous	±pilose ±glandular	glandular	glabrous	glabrous	±villous glandular	±pilose glandular	±pilose glandular
petioles	narrow	narrow	narrow	narrow	sessile	narrow	broad	sessile	sessile
Heads: type	radiate	radiate	discoid	radiate	radiate	radiate	discoid	discoid	discoid
number	1	1	3-10	5-15	3-5	1-3	3-9	1-7	10-20
shape	broadly campanulate	campanulate-turbinate	turbinate-campanulate	turbinate-campanulate	turbinate	campanulate-turbinate	turbinate-campanulate	turbinate-campanulate	narrowly turbinate
Phyllaries: shape	ovate-lanceolate	ovate-lanceolate	ovate-lanceolate	ovate-lanceolate	lanceolate	oblanceolate	broadly lanceolate	ovate-lanceolate	lanceolate
pubescence	pilose ±glandular	±pilose glandular	pilose glandular	glandular	±villous ±glandular	glandular	±villous glandular	pilose glandular	glandular
Pappus: color	white	white	white	white	white	white to tawny	white	white	white (tawny)
setae	barbellate	barbellate to subplumose	barbellate to subplumose	barbellate	barbellate	barbellate to subplumose	barbellate	barbellate	barbellate to subplumose
Achenes: color	dark grey	dark grey	dark grey	black	brown	dark grey	black	dark grey	dark grey
glandular hairs	+-	-	+	+	+-	+	+	-	+
duplex hairs	+	+	+	-(+)	-(+)	-	-	+	-
Chromosome number (2n)	38, 57, 76, 95 114	38	38, 57, 76	57, 76	38, 76	76	38, 76	38	38

ary trends will be given where appropriate. A synthesis of all the data accumulated in the present study, including morphology, will form the basis of a separate Phylogeny section.

Habit - All species of Austromontana are herbaceous perennials. With respect to underground parts, both A. venosa and A. viscosa possess a thick woody caudex at or below the soil surface, which gives rise to several flowering shoots. The remaining species possess slender rhizomes which give rise to both flowering shoots and numerous sterile basal rosettes of leaves (innovations). Both rhizomes and caudices are frequently covered with dark scales and old leaf bases which give them a thickened appearance. In A. gracilis the tip of the rhizome may have several branches, thus producing a many stemmed crown (approximate crown) with the flowering shoots appearing in dense clumps (Figure 5). In the present study the presence of the woody caudex is considered the derived or apomorphous condition. This is in agreement with Maguire's (1943) observation for the genus Arnica in general.

Stems - Stems in most species of subgenus Austromontana are usually simple or rarely branched. Arnica discoidea and A. venosa are sometimes several branched above the middle while A. viscosa is several branched throughout, sometimes so much that it resembles a small bush. In addition, virtually all species are much more branched when they occur on more exposed or disturbed sites. Maguire (1943) considered stem branching a derived condition in the genus Arnica. Results of the present study confirm this observa-

Figure 5 . Typical specimens of *A*. *gracilis* Rydb.



CARBON CO.: [illegible]
one fork of [illegible]
northeast of Glacier Lake, [illegible]
southwest of Red Lodge. [illegible]
E., about S. 27. Elev. about [illegible]
feet. Rays [illegible]

Arthur Cronquist [illegible] August [illegible]

tion for the subgenus Austromontana. The unbranched habit is here considered plesiomorphous while stem branching is considered apomorphous.

Stem height varies from 10-30 cm in the relatively small A. cernua and A. gracilis, up to 60-70 cm in robust specimens of A. discoidea and A. cordifolia. In general, stem pubescence resembles leaf pubescence, although it is usually denser above and reduced below.

Vestiture - Virtually all parts of all species of Austromontana are to some degree pubescent. Straley (1980) has given a detailed, complete and well illustrated account of the vestiture of Austromontana. Both long (1-2 mm) and short (0.1-0.2 mm) septate glandular and non-glandular hairs occur in the subgenus. The long stipitate glandular hairs have stalks 6-8 cells long while the short stalks are 2-3 cells long. Both are 2 cells thick. Arnica latifolia generally lacks glandular pubescence, A. viscosa has only the long type, A. gracilis has only the short type and the remaining species have both long and short. In A. viscosa the entire plant is densely covered with long stipitate glandular hairs, so much so that it feels slimy to the touch.

Non-glandular hairs are one cell thick and either long (1-3 mm) or short (0.3-0.5 mm).

Foliage - Although highly variable, characters of the leaves are generally the most reliable in distinguishing the species of Austromontana. Characters considered important in the present

study are leaf number, shape, margin, position and petiole width. Within the subgenus there is a general evolutionary trend from few, broad, coarsely dentate, narrowly petiolate leaves mostly below the mid-stem; towards many, narrower, entire margined, sessile, evenly distributed leaves.

The number of cauline leaves varies from 2 to 4 pairs in such species as *A. cordifolia* and *A. latifolia* to more than 25 in *A. viscosa*. Species intermediate between these extremes include *A. spathulata* (3-5), *A. discoidea* (3-7) and *A. venosa* (6-10). Additionally, in the few leaved species the leaves tend to be mostly below mid-stem while, in contrast, in the many leaved species they are evenly distributed along both the stems and branches. This appears to be a trend within the genus *Arnica* in general (Maguire, 1943).

Within the subgenus *Austromontana* there is a definite trend from broad, dentate leaves towards narrower, entire margined leaves. Leaf shape varies from broadly cordate in *A. cordifolia* to broadly lanceolate in *A. dscoidea*. Intermediate conditions include: ovate or ovate-elliptic in *A. cernua*, *A. latifolia*, *A. venosa* and *A. nevadensis*; spathulate in *A. spathulata* and ovate-oblong in *A. viscosa*. Leaf margins vary from coarsely dentate in the plesiomorphous *A. cordifolia* to entire in its derivative *A. nevadensis* and the highly apomorphous *A. viscosa*. Intermediate forms include crenate in *A. cernua* and serrate to serrate-dentate in the remaining species.

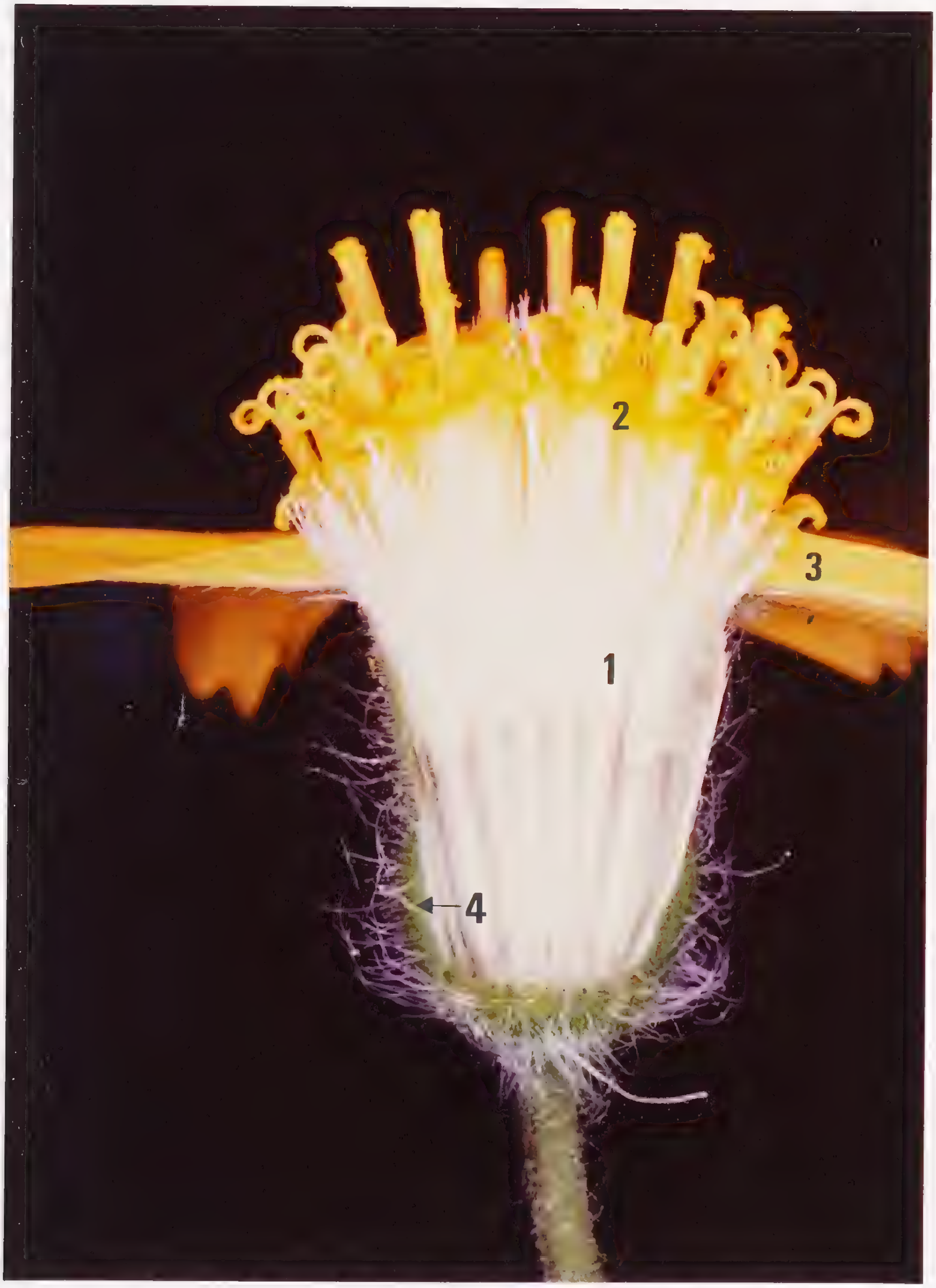
Within the subgenus *Austromontana* there is a distinct evolutionary trend in petiole width from narrow to broad to completely sessile leaves. The latter represents the apomorphous condition within the subgenus. Five of the nine species have narrowly petiolate leaves (*A. cordifolia*, *A. cernua*, *A. discoidea*, *A. nevadensis* and *A. gracilis*), three species have sessile leaves (*A. latifolia*, *A. venosa* and *A. viscosa*) while *A. spathulata*, with broadly winged petioles, represents the intermediate condition. Occasionally, the lower leaves of *A. latifolia* are short petiolate while the lower leaves of *A. cernua* and *A. gracilis* are infrequently narrowly winged. In addition, in all of the rhizomatous species, including the sessile leaved species, the leaves of the innovations are narrowly petiolate. The leaves of the innovations are otherwise similar to the cauline leaves. Additionally, in all species of the genus the upper leaves are often reduced, bract-like and not infrequently sub-opposite.

Inflorescence - The inflorescence of *Arnica*, like that of the Compositae in general, is a capitulum (head) consisting of an aggregation of sessile florets borne on a common receptacle and subtended by an involucre of bracts (phyllaries). Additionally, a ring of appendages, the pappus, is commonly borne upon the ovary. Characters of the inflorescence of *Austromontana* are illustrated in Figure 6.

Within the subgenus *Austromontana* several characters of the inflorescence are considered important in both the delimitation of

Figure 6 . Inflorescence of *Arnica cordifolia*.

1. Pappus
2. Disc floret
3. Ray floret
4. Phyllary


2
3
1
4

species and the determination of evolutionary relationships. Among these characters are head type (radiate vs. discoid), number and shape; phyllary shape and characters of the pappus. With the exception of *A. parryi* (subgenus *Chamissonis*) no discoid species of *Arnica* occur outside the subgenus *Austromontana*. Within the latter *A. viscosa*, *A. venosa*, *A. spathulata* and *A. discoidea* are discoid while the remaining are radiate. In addition, in *A. discoidea* some marginal disc florets may be ampliate (elongated and ray-like) resulting in some specimens of this taxon being confused with *A. cordifolia*. Results of the present study support Maguire's (1943) observation that the discoid condition represents the apomorphous state in *Austromontana*. Indeed, Cronquist (1977) considers the discoid condition to be apomorphous within the Compositae in general.

The number of ray florets varies from 5 to 15 while disc florets vary from 10 to 90. Within the subgenus there is a general trend of reduction in the number of disc florets, particularly in the discoid species. *Arnica cordifolia* and *A. latifolia*, with up to 90 disc florets represent the plesiomorphous condition while *A. viscosa*, with as few as 10 florets, is viewed as highly apomorphous.

Cronquist (1977) considers yellow colored corollas plesiomorphous within the Compositae in general. With the exception of *A. viscosa*, which has cream colored florets, all other *Arnica* species possess yellow corollas. Clearly, the cream colored florets of *A. viscosa* represent an apomorphous condition in *Austromontana*.

Within _Austromontana_ heads may occur singly as in _A. nevadensis_, _A. cordifolia_ and _A. cernua_ or, more commonly 3 to several heads are arranged in a corymbose influorescence. Species with several heads include _A. viscosa_ (10-20), _A. gracilis_ (5-15) and _A. discoidea_ (3-10, or up to 30). Maguire (1943) considered solitary heads plesiomorphic within _Arnica_ in general and Cronquist (1977) noted a similar trend towards increasing head number in the Compositae in general. In the present study, the solitary condition is considered plesiomorphous in _Austromontana_ while, in contrast, an increased number of heads is interpreted as a derived or apomorphous state.

The pappus in the genus _Arnica_ is composed of a ring of 25-70 capillary bristles of varying length. Based on seta length, Maguire (1943) has recognized three conditions within the genus: barbellate (0.1-0.2 mm), subplumose (0.2-0.35 mm) and plumose (0.35-0.6 mm). Also, within the genus pappus color varies from white to tawny. Maguire (1943) considered the white, barbellate pappus plesiomorphous while the tawny, plumose pappus was considered apomorphous. Most species of _Austromontana_ have retained the plesiomorphous white, barbellate pappus. However, in _A. cernua_, _A. discoidea_, _A. nevadensis_ and _A. viscosa_ the pappus is generally barbellate or less frequently subplumose. Additionally, in both _A. nevadensis_ and _A. viscosa_ the pappus is sometimes tawny.

Phyllaries - Although somewhat variable, characters of the involucral bracts are often quite helpful in delimiting species.

Phyllary shape varies from ovate-lanceolate (*A. cordifolia*, *A. cernua*, *A. discoidea*, *A. gracilis* and *A. venosa*) to lanceolate (*A. latifolia* and *A. viscosa*). *Arnica nevadensis* has distinctive oblanceolate phyllaries. Within the subgenus *Austromontana* the ovate-lanceolate condition is considered plesiomorphous while the lanceolate and oblanceolate shapes are considered apomorphous.

Phyllary vestiture, like that of the leaves, consists of various combinations of short and long stipitate glandular and non-glandular hairs. The vestiture is always densest and longest at the base of the bracts, at the point of their attachment to the peduncle (periclinum). The presence of only glandular hairs may represent the derived condition within *Austromontana* since the phyllaries of *A. gracilis*, *A. nevadensis* and *A. viscosa* (all considered apomorphous species) possess only glandular hairs.

Achenes - Achene color in *Austromontana* is mostly grey with the exception of *A. gracilis* (black), *A. spathulata* (black) and *A. latifolia* (brown). Length varies from 4.5-10 mm, with *A. gracilis* and *A. viscosa* being the shortest and *A. cordifolia* the longest. Achene width is almost uniformly 1 mm with the exception of *A. venosa* (1.5 mm). Achene vestiture, which is quite useful in delimiting species, consists of various combinations of both short and long glandular hairs and duplex (forked) hairs. For example, *A. viscosa* has only long stipitate glandular hairs, *A. gracilis* has a few short glandular hairs, *A. venosa* has an abundance of duplex hairs and *A. discoidea* has both duplex and glandular hairs.

Achene characters, particularly vestiture, are generally quite reliable in delimiting the species of _Austromontana_. However, few evolutionary trends are readily discernible. The dark grey color is probably plesiomorphous while brown and black probably represent derived conditions. Perhaps the presence of glandular hairs represents an apomorphous state since relatively apomorphous species such as _A_. _gracilis_, _A_. _nevadensis_ and _A_. _viscosa_ possess glandular hairs while plesiomorphous species such as _A_. _cordifolia_ and _A_. _latifolia_ generally lack them.

CHROMOSOME NUMBERS

Chromosome numbers have been determined for 146 populations of taxa within Austromontana (Table 5). It is apparent that the basic chromosome number of the subgenus is $x = 19$. Previous counts which differ from this basic number need to be reinvestigated. Some aneuploid numbers may be encountered within individual plants as a result of the high frequency of meiotic irregularities associated with apomictic reproduction. However, Stebbins (1971) noted that aneuploid clones are rarely formed in apomictic complexes. Adequate sampling techniques should, therefore, reveal the ploidy level of most populations. Therefore, as suggested by Barker (1966), and for purposes of discussion, previously reported numbers that do not conform to the basic number of $x = 19$ have been rounded off to the nearest multiple of 19.

Barker (1966) noted that polyploidy in Arnica, especially when associated with meiotic irregularities indicates apomictic reproduction. Straley (1980) has recently confirmed this observation for the species of Austromontana. Based on Barker's (1966) criterion of meiotic irregularity, all polyploids in the present investigation are probably apomictic. Various numbers of univalents, bivalents, multivalents and chains were observed at metaphase I and numerous lagging chromosomes and bridges formed during anaphase I. With the exception of one population of A. spathulata (S. Wolf 384, ALTA), all diploids exhibited normal meiosis. Due to

Table 5. New chromosome counts in *Arnica* subgenus *Austromontana*.

Taxon	n=	2n=	Location and voucher***
A. cernua	19		USA: CA: Humboldt Co.: Horse Mt., W471.
		38	USA: OR: Josephine Co.: Babyfoot Lake, W464.
A. cordifolia	19		CAN: BC: km 132 Haines Rd. W306; YT: Canol Rd., km 16, W507; Squanga Lk, W505. USA: OR: Wallowa Co.: Minam Park, W449; Hwy 3, 8 km S Wa. state line, W447.
		38	USA: ID: Lewis Co.: 10 km N Craigmont, W347.
		57	CAN: ALT: Mt. Park, P16; Crows Nest Pass, Tent Mt. F77122; Kananaskis Forest, Hunter Creek, F77102; km 90 Kananaskis Forestry Rd., F77120; YT: Skagway Rd., 19 km S. Carcross, W499*. USA: MT: Flathead Co.: 8 km E Bigford, W496*; Gallatin Co.: Targhee Pass, W433*; Lincoln Co.: 23 km W Libby, W444*; Missoula Co.: 34 km N Seeley Lk, W495*. WY: Albany Co.: 12 km W Centennial, W419*; Sublette Co.: 16 km NE Pinedale, W427*; Teton Co.: Togowotee Pass, W430*, W432*.

38 CAN: ALT: Jasper Nat. Park, Maligne Lk, D7846; Ghost River, 19 km N Morley, F77126; Mayberne Tower, 35 km NW Edson, E7801; km 4.6 Plateau Mt. Rd., W313; 14 km N Nordegg, F77128; Mt. Park, F77134; Kananaskis Forestry Rd.: km 64 F77110; km 129, W320; km 145, W308. BC: Skagway Rd., 65 km S Carcross, W500; Hwy 93: 26 km N Jct Hwy 3, W441; 11 km S Jct Hwy 3, W442; Hwy 3, 15 km E Osoyoos, B80055; Hwy between Pavillion and Clinton, B80060; km 133 Haines Rd., W304, W305. YT: Canol Rd., km 118, W508; Skagway Rd., 7 km S Carcross W498; 26 km S Haines Jct, W300; Haines Rd.: km 157, W303; km 177, W302.

USA: CA: Nevada Co.: W side Donner Lk, W476. ID: Custer Co.: 15 km W Challis, W486; Idaho Co.: km 20, Seven Devil's Rd., W354. MT: Lincoln Co.: 25 km S Eureka, W443; km 23 Mt. Marston Rd., W343; Missoula Co.: 10 km E Bonner, W493; 22 km W Lolo City, W491. NV: White Pine Co.: Wheeler Peak, W480. OR: Grant Co.: 72 km S Ukiah, W452; Umatilla Co.: 14 km S Ukiah, W451; Union Co.: Hwy 204, 23 k N Elgin, W366; 40 km E Ukiah, W450; Wallowa Co.: km 12 Hurricane Creek Trail, W365; Wallowa State Park, W362; 25 km N Enterprise, W448; Wheeler Co.: Ochoco Summit, W453. UT: Beaver Co.: 23 km E Beaver, W482; Cache Co.: Beaver Mt., W484; Iron Co.: 17 km E Cedar City, W481; Rich Co.: Bear Lake Summit, W485; Utah Co.: Mt. Timpanogos, 483. WA: Asotin Co.: Field Springs Park, W446; Chelan Co.: Swauk Pass, W368; Spokane Co.: Mt. Spokane, W445.

	76	CAN: ALT: Elk Pass, W Kananaskis Lake, F77148; 32 km N Nordegg, F77104; Kananaskis Lake F77145; Hunter Creek, Kananaskis Forest, F77101. USA: CA: Plumas Co.: Gold Lake, W477. CO: Chaffee Co.: Hwy 306, 23 km W Buena Vista, W410; Summit Co.: Hwy 9, 4.5 km S Breckenridge, W413. ID: Lemhi Co.: 5 km S Gibbonsville, W487. MI: Keweenaw Co.: M *s.n.* MT: Deerlodge Co.: Storm Lake, W435; Missoula Co.: Marshall Ski Area, W492. OR: Klamath Co.: Parker Mt. Summit, W454; Wallowa Co.: 45 km N Hwy 86 on Forestry Rd. to Joseph, W361. UT: Duchense Co.: Hwy 33 at S border of Ashley Nat. Forest, W396; km 15 Blind Stream Rd. NW Hanna, W398; San Pete Co.: Jct Spring City-Skyline Drive Rd., W393. WA: Okanogan Co.: 23 km W Twisp, W509. WY: Teton Co.: Teton Nat. Park, Hidden Falls, W429.
	95	USA: CO: Pitkin Co.: 16 km W Independence Pass, W399.
A. discoidea	19	USA: CA: Humboldt Co.: 6 km Briceland, W472; Mendicino Co.: 14 km W Boonesville, W474; San Mateo Co.: Kings Mt., W475; Siskiyou Co.: Baldy Mt., W466; Trinity Co.: 3 km E Burnt Ranch, W470.
	38	USA: CA: Humboldt Co.: 5 km NW Orleans, W389; Trinity Co.: Hobo Gulch Rd., 22 km N Hwy 299, W390.

	57**	USA: CA: Plumas Co.: Gold Lake, W477*.
	38	USA: CA: Lake Co.: 13 km E Lower Lake, W473; Plumas Co.: E side Lake Almanor, W392.
A. gracilis	38	CAN: ALT: km 148 Kananaskis Forestry Rd., W324. USA: ID: Idaho Co.: Seven Devils Lake, W350.
A. latifolia	19	CAN: ALT: Banff Nat. Park, Moraine Lake, W513; Plateau Mt. Rd.: km 1.4, W314; km 4.6, W319; km 148 Kananaskis Forestry Rd., W321, W322. USA: CO: Clear Creek Co.: Loveland Pass, W416. ID: Idaho Co.: Seven Devils Lake, W352; Valley Co.: Lick Creek Summit, W357. MT: Lincoln Co.: km 22 Mt. Marston Rd., W344. OR: Clackamas Co.: Mt. Hood, W380; Curry Co.: Iron Mt., W457. WA: Clallam Co.: Olympic Nat. Park, Hurricane Ridge, W372; Okanogan Co.: Washington Pass, W369; Pierce Co.: Mt. Rainier Nat. Park: 1.6 km E Paradise Jct, W376; km 2.4 Paradise Trail, W375; Yakima Co.: 3.2 km E Mt. Rainier Nat. Park, W377. WY: Albany Co.: 13 km W Centennial, W424.
	38	USA: AK: Hatcher Pass, W503. OR: Clatsop Co.: Saddle Mt., W379. UT: Duchesne Co.: km 15 Blind Stream Rd., NW Hanna, W397. WA: Chelan Co.: Swauk Pass, W367; Kittitas Co.: Snoqualmie Summit, W510. WY: Teton Co.: Togwotee Pass, W431.

	38	CAN: ALT: Waterton Nat. Park, Goat Lake, D7830; Lynx Creek, 13 km S Belevue, F77123. USA: CA: Siskiyou Co.: Bolan Lake, W465; 13 km W Etna, W467. ID: "Idaho Co.: Lolo Pass, W490;" Lemhi Co.: 9 km S Lost Trail Pass, W488; Valley Co.: 3.2 km S Lick Creek Summit, W360. MT: Flathead Co.: Glacier Nat. Park, Hidden Lake, W489; Seeley Lake, W494.
	76	CAN: ALT: Waterton Nat. Park, Carthew Mt., W440. USA: MT: Deerlodge Co.: Storm Lake, W436.
A. nevadensis	38	USA: OR: Klamath Co.: Crater Lake Nat. Park: Garfield Peak, W382; Rim Trail, W381.
A. spathulata	19	USA: CA: Del Norte Co.: 5.8 km NW Patrick, W387; French Hill, W458; 10 km N Gasquet, W459. OR: Josephine Co.: Babyfoot Lake, Siskiyou Nat. Forest, W384; Hugo, W455; Merlin, W456; Selma, W463; Store Gulch Guard Station, W462.
	38	USA: OR: Josephine Co.: 17 km N Partrick, W460; 20 km N Patrick, W461.
A. venosa	19	USA: CA: Shasta Co.: Hwy 5, 3 km S Gibson turnoff, W468; Shasta Bally Rd., S Brandy Creek, W469.

A. viscosa	19	USA: CA: Siskiyou Co.: Horse Camp, Mt. Shasta, W391. OR: Klamath Co.: Crater Lake Nat. Park, Garfield Peak, W511.

* Count based on meiotic cells

** New count for this taxon.

*** Abbreviations of collectors: B = J.F. Bain; D = H. Dudynsky; E = R.E. Ellis, F = J. Forbes; J = S.J. Wolf, K.E. Denford and H. Dudynsky; M = Michigan Nature Association; P = W.L. Peterson; W = S.J. Wolf.

the broad nature of the present investigation and the complexity of chromosome behavior in *Austromontana*, no attempt was made at cytogenetical analysis.

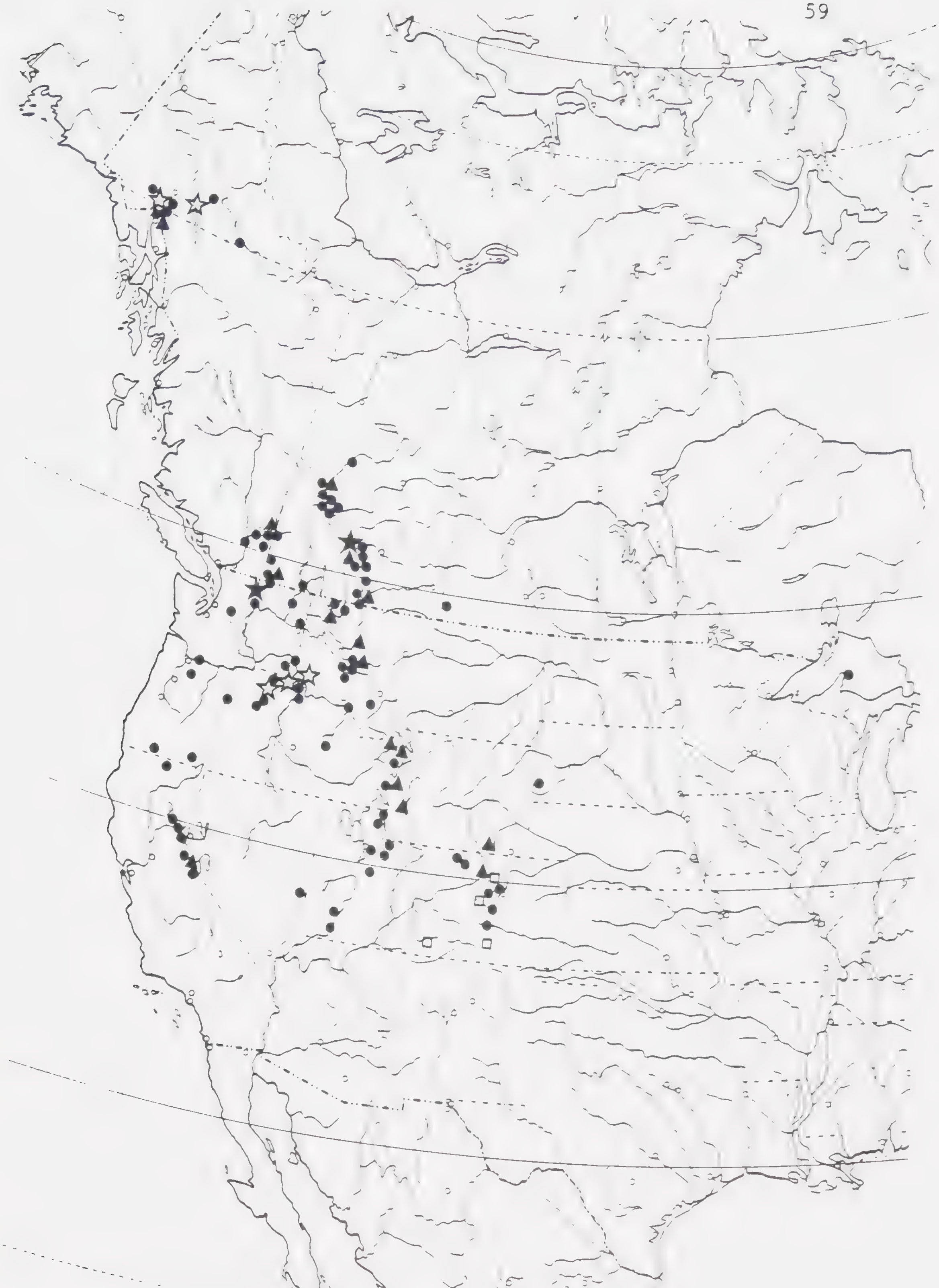
A. cernua - this species is a rare serpentine endemic of the Klamath region of southwest Oregon and northwest California known only from about 30 populations. Three diploid counts for this taxon have previously been reported (Table 2) and results of the present investigation indicate that it is probably entirely diploid ($2n = 38$).

A. cordifolia - this is one of the most widely distributed species of *Arnica*, ranging from Alaska to New Mexico and California with disjunct populations in Ontario and adjacent Michigan. Previous reports (Table 2) have indicated that this taxon is cytologically diverse with all ploidy levels from diploid through hexaploid being reported. Including the 83 new counts presented in Table 5, a total of 137 populations representing virtually the entire range of this species have been sampled for chromosome number. A map depicting the distribution of these populations is presented in Figure 7.

Prior to the present investigation only one diploid population was known for *A. cordifolia*. Six new diploid populations have been located in the present study: 3 in the Yukon Territory and adjacent British Columbia, 2 in northeast Oregon and 1 in northern Idaho. A total of 23 triploid populations have been located. In general, the triploid condition is restricted primarily to the

Figure 7. Distribution of the chromosome races of *A*. *cordifolia*.

☆ -2*n*, ▲-3*n*, ● -4*n*, □ -5*n*, ★ -6*n*.



front ranges of the Rocky Mountains. The large majority of *A. cordifolia* populations are tetraploid throughout the entire range of this taxon. All three populations sampled from Michigan are also tetraploid. Three previous pentaploid populations of *A. cordifolia* have been reported from Colorado. An additional pentaploid population of this taxon, also in Colorado, has been located in the present study. Straley (1980) has reported 2 hexaploid populations of *A. cordifolia*, one in central Washington and the other at Vermillion Pass, Alberta.

Maguire (1943) observed that *A. cordifolia* exhibits little morphological variability when it occurs in its normal woodland habitat; however, when the plants occur in such transition areas as the newly disturbed soil of road banks, it shows a great deal of variability. Maguire noted that the leaves become smaller, narrower and lose their cordate bases; the pubescence becomes denser, harsher and more glandular and the plants become smaller and more branched. Almost without exception, the triploids reported in Table 5 exhibit these characteristics and were all collected in disturbed open habitats, particularly road banks. Maguire (1943) noted that, "it is to these diverse biotypes that the greater number of specific names have been applied." The great degree of morphological divergence between these populations and woodland populations, their preference for disturbed habitats, and triploid condition suggest they may be hybrids between different populations or taxa.

Grant (1971) noted that permanent odd polyploidy and apomixis are means of preserving adaptively valuable hybrid products. Stebbins (1971) noted that since irregular meiosis in apomicts is not a barrier to seed formation, odd polyploids can be as successful as their even polyploid congeners. Barker (1966) and Straley (1980) have shown that _A_. _cordifolia_ is apomictic throughout its entire range. This mode of reproduction coupled with the triploid condition in these populations is possibly the result of stabilizing selection to preserve an advantageous hybrid product that has exploited a new niche. However, it should also be noted that the morphological anomalies of these populations may merely be the result of the open disturbed habitat rather than the triploid condition.

Stebbins (1971) suggested that most mature polyploid complexes originated during the Pleistocene or late Pliocene and have the following characteristics: the diploids are rare and of scattered occurrence; the most widespread polyploid level is the tetraploid, and higher ploidy levels, when present, are both fewer in number and more restricted in distribution. _Arnica_ _cordifolia_ represents a classic mature polyploid complex: tetraploids are widespread throughout its entire range, only six widely scattered diploid populations are known, triploids occur mainly in the front ranges of the Rocky Mountains, pentaploids are known only from Colorado and two hexaploid populations have been reported.

A. discoidea - This taxon, the most widely distributed of the discoid species; ranges from the Columbia River Gorge in southern Washington south to Orange County, California. Twenty populations of this taxon have been sampled for chromosome number (Tables 2, 5). It contains both diploid and tetraploid races and one triploid race (newly reported in the present study). In general, the diploid races tend to occur within the center of distribution of this taxon while the tetraploids occur at the periphery, e.g., Klickitat Co., Washington and Wasco Co., Oregon in the north and Orange Co., California in the south. The triploid race may have been derived through hybridization of diploid and tetraploid races, however, it is also possibly the result of hybridization between a diploid A. discoidea and tetraploid A. cordifolia. The triploid population was collected amongst a tetraploid population of A. cordifolia that had flowered about one month earlier. Such temporal isolation of parent and hybrid progeny could allow the hybrids to persist. If the two taxa are as closely related as previously suggested by Maguire (1943), then hybridization between them may indeed be possible. Results of the present study do indeed indicate that A. discoidea is derived from A. cordifolia. Further evidence to support this view will be presented in subsequent sections.

A. gracilis - this species occupies high montane to alpine regions of southern British Columbia and Alberta through Oregon and Wyoming. Five triploid and one tetraploid population have been previously reported for this taxon (Table 2). Two additional

tetraploid populations have been located in the present study (Table 5). Straley (1980) suggested that this taxon may be a hybrid between *A. latifolia* and either *A. mollis* Hook. or *A. diversifolia* Greene. Results of the present investigation, to be presented in subsequent sections, do indeed suggest that *A. gracilis* is probably derived from *A. latifolia*.

A. latifolia - this taxon is one of the most widely distributed arnicas in western North America, occurring from Alaska to Colorado and California. Prior to the present investigation, this taxon was considered to be almost entirely diploid with only one tetraploid population known (Straley, 1980). Results of the present investigation (Table 5) indicate that *A. latifolia* is predominantly diploid throughout its range; however, several tetraploid populations have been located in northwestern Montana, adjacent Alberta, and Idaho. In addition, two tetraploid populations have been located in the Klamath region.

A. nevadensis - previously, 3 tetraploid populations have been reported for this taxon (Table 2) which is largely restricted to the Cascades and Sierra Nevada. Two additional tetraploid populations have been located in the present study (Table 5).

A. spathulata - this species is a rare serpentine endemic of the Klamath region. With the exception of one tentative tetraploid count by Barker (1966), all previous counts have been diploid (Table 2). Ten new counts are reported in the present study, 8 of which are diploid and 2 of which are tetraploid (Table 5).

A. venosa - this taxon is probably the most geographically restricted species of *Arnica*. All known populations occur within a 20 km radius of Shasta Lake in Shasta County, California. Four populations have been sampled for chromosome number and all are diploid (Tables 2, 5)

A. viscosa - this species is a very rare endemic known only from seven locations at high elevations on a few volcanic peaks in southern Oregon and northern California. Three of these populations have been sampled for chromosome number and all are diploid (Tables 2, 5).

Within *Austromontana* in general, the more geographically widespread taxa tend to have higher and more diverse chromosome numbers while the narrow endemics tend to be diploid. *Arnica cordifolia*, the most widespread species, has 5 chromosome races ranging from diploid ($2n = 38$) through hexaploid ($2n = 114$). This taxon has been recognized as a mature polyploid complex (*sensu* Stebbins, 1971). *Arnica latifolia* is predominantly diploid with several tetraploid populations restricted to northwest Montana and adjacent regions. *Arnica gracilis* has both triploid and tetraploid races. *Arnica nevadensis* is wholly tetraploid. *Arnica discoidea*, the most widespread of the discoid species, has diploid, triploid and tetraploid populations. The narrow endemics of the Klamath region; *A. cernua*, *A. venosa* and *A. viscosa* are wholly diploid while *A. spathulata* is predominantly diploid with only 2 tetraploid populations reported.

FLAVONOID CHEMISTRY

A total of 26 flavonoids, including 12 glycosides and 14 free aglycones, have been isolated and characterized from Austromontana. Chromatographic and spectral data for these compounds are presented in Tables 6 and 7, structures are given in Figures 8 and 9 and a two-dimensional chromatogram of the glycosides is presented in Figure 9.

The subgenus exhibits a wide array of both simple and highly complex compounds including the simple flavonols Kaempferol and Quercetin, simple flavones Apigenin and Luteolin, mono-methyl ethers of all these compounds and highly methylated derivatives of the flavones Apigenin and Luteolin. The distribution of these compounds in the various taxa investigated is present in Table 8. In addition to exhibiting interspecific variability, the distribution of compounds varied greatly with respect to geographic distribution. Following a general discussion of the major flavonoid constituents, the specific chemistry of each species will be discussed.

The most frequently occurring compound, found in 87 of 89 populations, is Viscosin, here named for A. viscosa, the first species from which it was isolated. Spectral data and color characteristics of both glycoside and aglycone and the products of hydrolysis (Quercetin and glucose) indicate that it is a 3-0 glucoside of Quercetin. However, its Rf's, particularly in phenol (0.26), are unlike any Quercetin 3-glucoside previously reported.

Table 6. Chromatographic, spectral and R_f data for the flavonoid aglycones of *Arnica* subgenus *Austromontana*[1].

Compound	MeOH (λmax, nm)	NaOMe (λmax, mn)	ALCL$_3$ (λmax, nm)	ALCL$_3$-HCL (λmax, nm)	NaOAc (λmax, nm)	NaOAc-H_3BO_3 (λmax, nm)	(Colours at 350nm[3])			Rf's x 100[2]			
							UV	UV/NH_3	UV/NA	BAW	H_2O	15%HOAc	PhOH
Apigenin	336 285s[6] 268	385↑[5] 346 274	384 346 302 276	380 342 300 276	380 273	338 268	P	YG	Y	90	-	09	85
A 6-Me	335 273	390↑ 322 276	356 300 284s	350 300 284s 264s	376 300 275	338 275	P	G	G	90	-	10	90
A 7-Me	330 302 284s	390↑ 302s 278 242	386 346 301 277	384 342 301 277	390 344 298s 271	340 269	P	YG	G	90	-	10	92
A 6, 7-di Me	332 276	388↑ 305s 278	357 300 262s	353 300 262s	388 274	336 274	P	G	G	80	-	08	68
Luteolin	350 268 253 240s	401↑ 324s 268s	430 324 296s 276	385 350 294s 274	386 324s 268	425s 368 296s 258	P	Y	O	80	-	03	70
L 6-Me	341 268 256	400 270	402 272	359 275 260	392 268	356 262	P	G	O	85	-	04	86
L 4'-Me	344 269 256	390↓ 273	392 364 294 276	385 358 292 277	370 274	350 270	P	P	Y	88	-	06	93
L 6OH, 4'-Me	337 285	370→ 286 245s	362 304 380s	354 302 280s	398s 336 284	339 284	P	P	Y	89	-	06	97
L 6, 4'-di Me	342 268	370→ 278	365 300s 278 262	360 300s 278 258	350 269	341 268	P	P	YG	86	-	11	95
L 3', 6, 7-tri Me	346 292 268, 253, 242s	389↑ 302s 268	386s 359 296s, 276, 260	382s 354 296s, 276, 260	406 356 290s, 264, 258	346 268 252	P	Y	YG	78	-	10	82
Kaempferol	366 298s 269 258s	412↓ 320 276	428 360 306s 270	426 358 306s 271	386 302 275	368 270	Y	Y	G	86	-	04	60
K 6-Me[4]	366 270	438↑ 325s 285	426 370 306s 272	426 365 306s 272	386 310s 275	368 270	Y	Y	G	70	-	05	?
Quercetin[4]	370 300s 270s 256	322↓	450 306s 272	424 360 302s 268	394 328 274	388 300s 262	Y	Y	O	65	-	03	32
Q 3-Me	358 268s 256	420↑ 338s 279	410 364 298s 268	398 360 298s 266	390 270	378 261	P	Y	O	70	-	04	58
Q 6-Me (Patuletin)	365 258	425 334s 250	442 270	414 267	396 268	386 264	Y	YG	O	86	-	04	90
Q 3', 6di Me	350 266s 258	432↑ 352 272	414 354 302s 270	400 349 302s 266	380 265	360 265	Y	Y	Y	88	-	05	82

[1] Abbreviations: A = Apigenin, L = Luteolin, K = Kaempferol, Q = Quercetin, glu = glucose, gal = galactose, Me = methoxyl.

[2] See text for solvent composition.

[3] Colour key: P = purple, Y = yellow, G = green, O = orange. NA refers to Naturstoffreagens A in MeOH.

[4] Present only as a product of hydrolysis of glycosides.

[5] ↑ - increase in intensity, ↓ - decrease in intensity, → - no change in intensity.

[6] s - shoulder

Table 7. Chromatographic, spectral and R_f data for the flavonoid glycosides of Arnica subgenus Austromontana[1].

Compound	MeOH (λmax, nm)	NaOMe (λmax, nm)	AlCl$_3$ (λmax, nm)	AlCl$_3$-HCl (λmax, nm)	NaOAc (λmax, nm)	NaOAc H$_3$BO$_3$ (λmax, nm)	(Colours at 350nm[3]) UV	UV/NH$_3$	UV/NA	Rf's x 100[2] BAW	H$_2$O	15%HOAc	PhOH	Aglycone	Sugar
A 7-O-glu	332 268	382↑ 301s 272	385 350 298 276	383 346 298 276	388 267 255s	339 267	P	YG	G	64	04	24	80	A	glu
L 7-O-glu	350 268s 255	396↑ 296s 264	435 330 296s 275	390 360 296s 274	408 360s 264s 258	370 256	P	Y	O	46	01	14	59	L	glu
L 6-Me, 7-O-glu	341 269s 257	402↑ 270s	408 270	359 270	402 350s 266	360 262	P	Y	O	49	01	17	65	L 6-Me	glu
K 3-O-glu	346 270	400↑ 328 278	412 362 296s 273	410 360 295s 275	378 300s 273	347 270	P	G	G	71	13	42	82	K	glu
K 3-O-gal	347 268	400↑ 328 276	400 356 302s 278	400 356 302s 277	388 302 272	346 269	P	G	G	58	10	53	87	K	gal
K 6-Me, 3-O-glu	346 270	396↑ 328 274	362 308s 277	356 304s 279	372 302 273	348 270	P	YG	G	62	34	45	47	K 6-Me	glu
Q 3-O-glu	358 258	408↑ 330 272	434 302s 274	394 360 302s 268	388 268	376 261	P	Y	O	58	09	39	55	Q	glu
Viscosin (Q 3-O-glu)	358 267s 258	414↑ 278	418 304s 270	394s 362 304s 268	390 270	376 263	P	Y	O	50	21	36	26	Q	glu
Q Gentiobioside	352 268s 258	415↑ 281	412 272	382s 368 266	388 336s 272	374 264	P	YG	O	40	24	43	33	Q	glu
Patuletin 3-O glu (Q 6 Me, 3-O-glu)	353 268s 258	408↑ 336 274	435 306s 274	380 306s 268	390 326s 272	370 265	P	YG	O	58	10	45	65	Q 6-Me	glu
Viscosa # 10 (L 7-di-glu?)	342 270	432↓ 270	436 276	398s 368 269	424 270	376 268	P	YG	O	24	12	65	55	?	glu
Viscosa # 11	330 272	408↑ 362s 276	396s 360 302s 275	396s 356 300s 275	400s 338 270	356 270	P	YG	G	36	13	58	72	?	glu gal

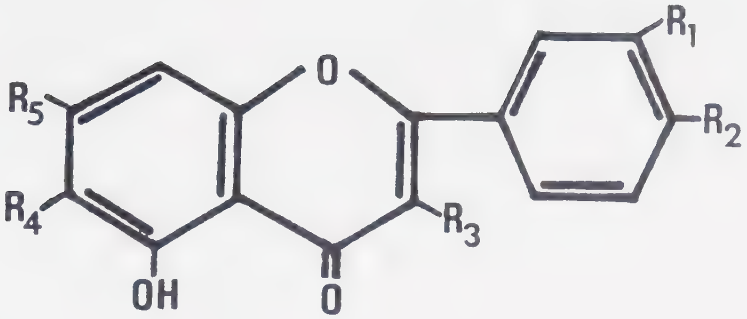
1 Abbreviations: A = Apigenin, L = Luteolin, K = Kaempferol, Q = Quercetin, glu = glucose, gal = galactose, Me = methoxyl.

2 See text for solvent composition.

3 Colour key: P = purple, Y = yellow, G = Green, O = orange. NA refers to Naturstoffreagens A in MeOH.

4 ↑ - increase in intensity, ↓ - decrease in intensity, → no change in intensity.

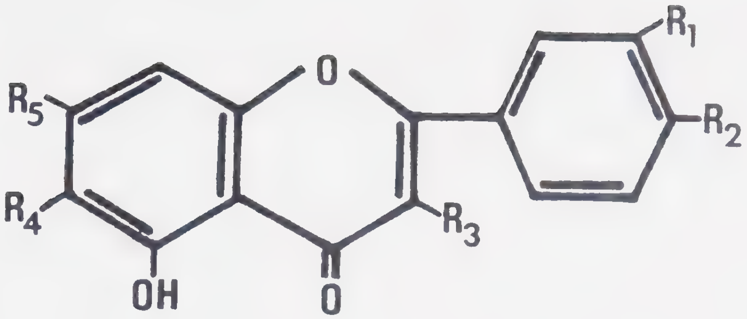
5 s - shoulder.



Compound	R_1	R_2	R_3	R_4	R_5
Apigenin	H	OH	H	H	OH
A* 6-Me	H	OH	H	OCH_3	OH
A 7-Me	H	OH	H	H	OCH_3
A 6,7-Me	H	OH	H	OCH_3	OCH_3
Luteolin	OH	OH	H	H	OH
L 6-Me	OH	OH	H	OCH_3	OH
L 4'-Me	OH	OCH_3	H	H	OH
L 6OH, 4'Me	OH	OCH_3	H	OH	OH
L 6,4'-di Me	OH	OCH_3	H	OCH_3	OH
L 3',6,7-tri Me	OCH_3	OH	H	OCH_3	OCH_3
Kaempferol	H	OH	OH	H	OH
Q 3-Me	OH	OH	OCH_3	H	OH
Q 6-Me	OH	OH	OH	OCH_3	OH
Q 3',6-di Me	OCH_3	OH	OH	OCH_3	OH

*Abbreviations: A-Apigenin, L-Luteolin, K-Kaempferol, Q-Quercetin.

Figure 8 . Structures of flavonoid aglycones of _Arnica_ subgenus _Austromontana_.



Compound	R_1	R_2	R_3	R_4	R_5
A* 7-0-glu	H	OH	H	OH	0-glu
L 7-0-glu	OH	OH	H	H	0-glu
L 6-Me, 7-0-glu	OH	OH	H	OCH_3	0-glu
K 3-0-glu	H	OH	0-glu	H	OH
K 3-0-gal	H	OH	0-gal	H	OH
K 6-Me, 3-0-glu	H	OH	0-glu	OCH_3	OH
Q 3-0-glu	OH	OH	0-glu	H	OH
Viscosin	OH	OH	0-di-glu**	H	OH
Q-Gentiobioside	OH	OH	0-di-glu***	H	OH
Q 6-Me, 3-0-glu	OH	OH	0-glu	OCH_3	OH

*Abbreviations: A-Apigenin, L-Luteolin, K-Kaempferol, Q-Quercetin, glu-glucose, gal-galactose.

**Sugar linkage undetermined.

***6-0-β-D-glucosyl-D-glucose.

Figure 9 . Structures of flavonoid glycosides of *Arnica* subgenus *Austromontana*.

Figure 10. 2-Dimensional chromatograph of the flavonoid glycosides of *Arnica* subgenus *Austromontana*. 1. *A. viscosa* #10. 2. *A. viscosa* # 11. 3. Quercetin Gentiobioside. 4. Luteolin 6-Me 7-O-glucoside. 5. Luteolin 7-O-glucoside. 6. Kaempferol 3-O-galactoside. 7. Quercetin 6-Me 3-O-glucoside. 8. Viscosin. 9. Kaempferol 6-Me 3-O-glucoside. 10. Quercetin 3-O-glucoside. 11. Apigenin 7-O-glucoside. 12. Kaempferol 3-O-glucoside.

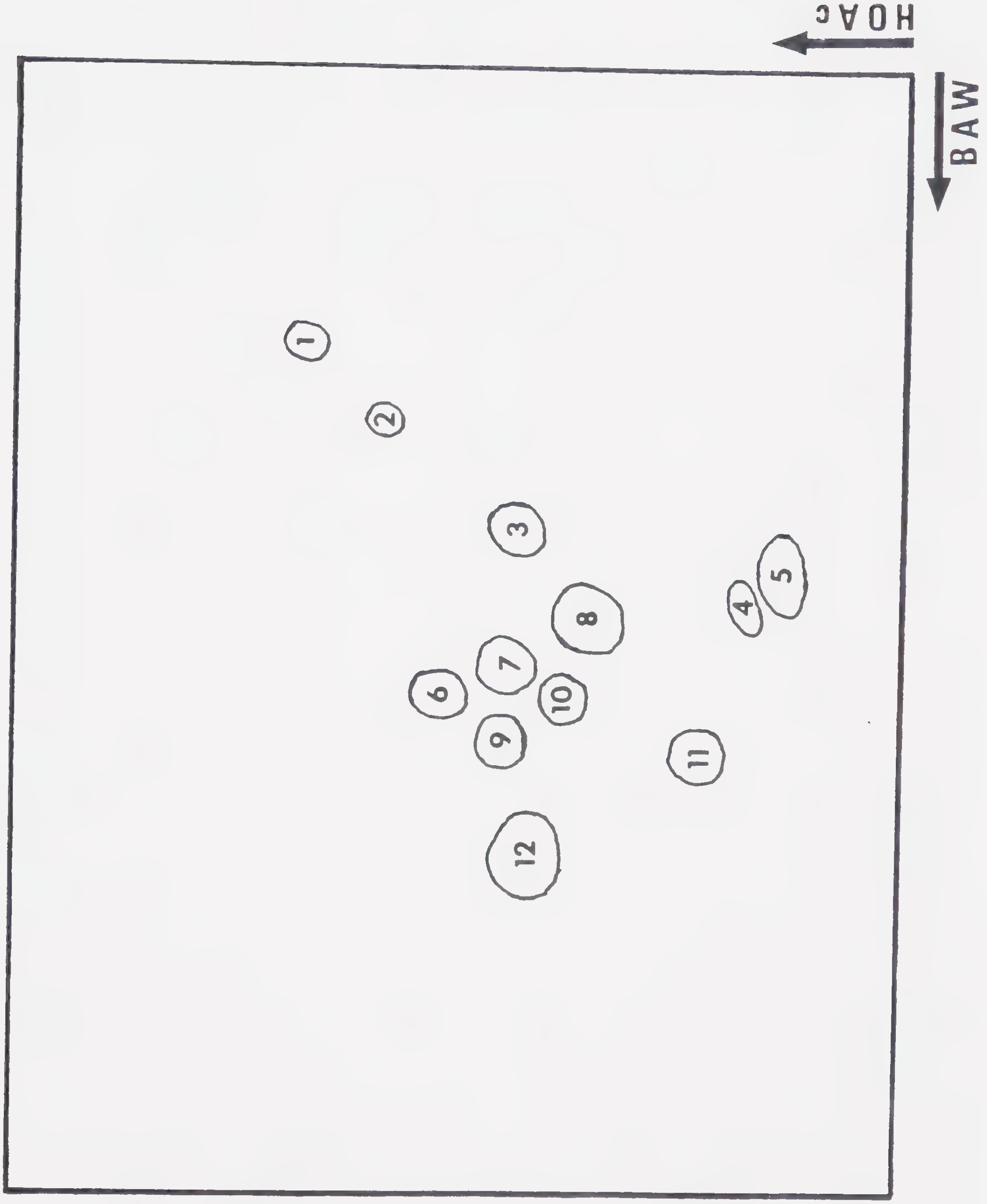

HOAc
BAW

Table 8. Distribution of flavonoids in the nine species of Arnica subgn. Austromontana.*

	A. cordifolia (33)**	A. cernua (2)	A. discoidea (11)	A. gracilis (2)	A. latifolia (26)	A. nevadensis (2)	A. spathulata (9)	A. venosa (2)	A. viscosa (2)	Total (89)
Apigenin			4						2	6
A 6-Me	24***		10	1	13	2	6	2	2	60
A 7-Me	1		4				1	2	2	10
A 6, 7-di Me			6						2	8
Luteolin				1						1
L 6-Me				2		2				4
L 4'-Me				1		2				3
L 6OH, 4'-Me									2	2
L 6, 4'-di Me			3				4		2	9
L 3', 6, 7-tri Me									2	2
Kaempferol					2					2
Q 3-Me	2			2						4
Q 6-Me				2	2					4
Q 3', 6-di Me									2	2
A 7-0-glu				2						2
L 7-0-glu	14		3	2						19
L 6-Me, 7-0-glu	6		2	1						9
K 3-0-glu	14	2	11	1	2		6	2	2	40
K 3-0-gal				2	17					19
K 6-Me, 3-0-glu	19		8	1			9	2		39
Q 3-0-glu	18		9	2	12	2	3		2	48
Viscosin	32	2	11	1	26	2	9	2	2	87
Q-Gentiobioside	33	2	11	1	26	2	9	2	2	86
Q 6-Me, 3-0-glu				2	18				2	22
A. viscosa #10									2	2
A. viscosa #11									2	
Total Compounds/ Taxon	10	3	12	16	9	6	8	6	15	26

*Abbreviations: A-Apigenin, L-Luteolin, K-Kaempferol, Q-Quercetin, Me-methoxyl, glu-glucoside, gal-galactoside.

**Numbers in parenthesis represent numbers of populations surveyed.

***Represents number of populations containing given compound.

Quercetin Gentiobioside (Quercetin 3-0-6-0-β-D-glucosyl-D-glucose) is another frequently occurring compound in _Austromontana_, present in 86 populations. This compound is easily identified by its Rf's, particularly in phenol (0.36), and the products of acid hyrolysis (Quercetin and glucose). Other common glycosides are Quercetin 3-0-glucoside (48 populations) and Kaempferol 3-0-glucoside (40 populations). These two compounds are the 2 most common glycosides found in the Compositae (Harborne, 1967) and have been. found in all other _Arnica_ species examined (Robins, 1977).

The most frequently occurring free aglycone in _Austromontana_ is Apigenin 6-methyl ether (Hispidulin), found in 60 populatons. Confirmation of the identification of this compound was by comparison of Rf and spectral data with that of Mues _et_ _al._ (1979).

According to Harborne (1977) this compound occurs frequently in the Compositae. The identification of 2 methylated aglycones, Apigenin 7-methyl ether and Apigenin 6,7-di-methyl ether was confirmed by Mass Spectral analysis in conjunction with Rf and UV spectral data. The former exhibited a molecular weight of 284 indicating 2-OH groups and 1-OCH_3 group while the latter had a molecular weight of 314 indicating 2-OH groups and 2-OCH_3 groups.

_A_. _cordifolia_ - A total of 10 flavonoids (7 glycosides and 3 aglycones) were found in a wide geographical sampling of 33 populations of _A_. _cordifolia_ (Table 9). The glycosides Quercetin Gentiobioside (33 populations) and Vicosin (32 populations) were ubiquitous or nearly so while Quercetin 3-0-glucoside (18 popula-

Table 9. Distribution of flavonoids in *A. cordifolia* populations surveyed.*

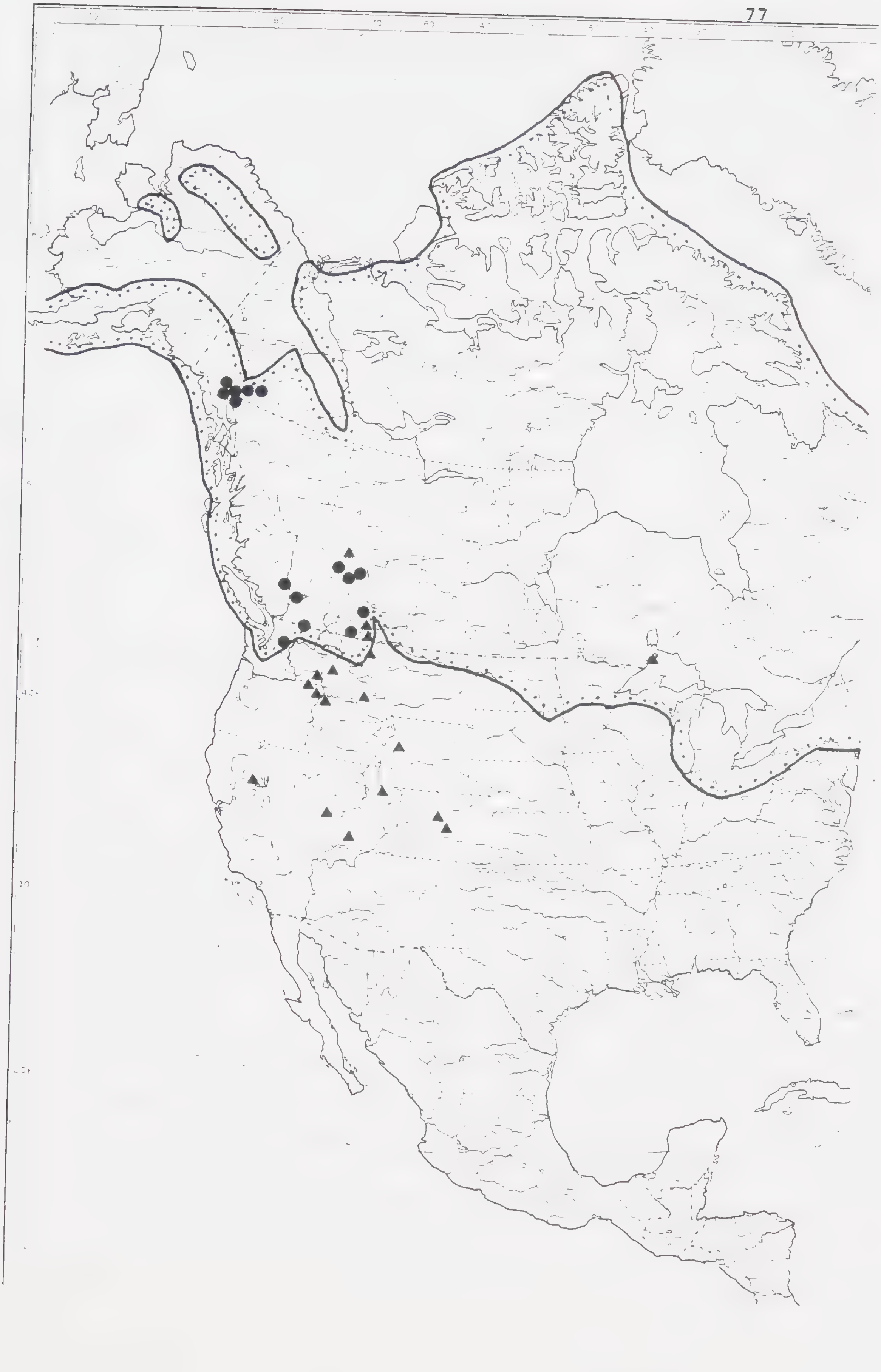
Location	Chromosome number (2n)	Collection number	A 6-Me	A 7-Me	Q 3-Me	Q-Gentiobioside	Viscosin	K 6-Me, 3-O-glu	Q 3-O-glu	K 3-O-glu	L 6-Me, 7-O-glu	L 7-O-glu
ALT	57	F77122				+	+					
ALT	57	F77102				+	+				+	+
ALT	76	F77104				+	+					+
ALT	76	E7801				+	+	+				
ALT	76	W308	+			+	+	+	+			
ALT	76	D7846				+	+					+
ALT	76	F77134				+	+	+	+		+	+
BC	?	B80052	+		+	+	+	+	+	+	+	+
BC	38	W306				+	+	+	+	+		+
BC	76	W304				+	+	+		+	+	+
BC	76	B80060	+			+	+	+	+		+	+
BC	76	B80055	+			+	+					+
BC	76	W441	+			+	+					+
CA	76	W476	+	+		+	+	+		+		
CO	76	W413	+			+	+		+			
CO	95	W399	+			+	+			+		
ID	38	W347	+			+						
ID	76	W354	+			+	+		+			
MT	57	W496	+			+	+		+	+	+	
MT	76	W435	+			+	+	+	+	+		
NV	76	W480	+			+	+	+	+	+		
ONT	?	S1849	+			+	+			+		
OR	38	W447	+		+	+	+	+	+			
OR	76	W448	+			+	+		+	+		
UT	76	W398	+			+	+	+	+			
UT	76	W481	+			+	+			+		
WA	76	W368	+			+	+	+		+		+
WA	76	W446	+			+	+	+	+	+		
WY	57	W430	+			+	+			+		
YT	38	W505	+			+	+	+	+			+
YT	38	W507	+			+	+	+	+			+
YT	57	W499	+			+	+	+	+			+
YT	76	W498				+	+	+	+		+	+

*Abbreviations: A-Apigenin, L-Luteolin, Q-Quercetin, K-Kaempferol, Me-Methoxyl, glu-glucoside.

tions) and Kaempferol 6-methyl ether-3-0-glucoside (19 populations) were randomly distributed throughout the entire range of this taxon. Kaempferol 3-0-glucoside (14 populations) is generally lacking from most northern populations. Except for a few populations in southern Alberta, Luteolin 7-0-glucoside (14 populations) is restricted to populations which occur near or north of the limits of maximum Pleistocene glaciation (Figure 11). In addition, Luteolin 6-methyl ether-7-0-glucoside is found in 6 of these 14 populations. Arnica cordifolia elaborates a very limited number of simple methyl ethers. Apigenin 6-methyl ether (24 populations) is distributed throughout most of its range, with the exception of southern Alberta and British Columbia. Two other methylated aglycones, Apigenin 7-methyl ether (1 population) and Quercetin 3-methyl ether (2 populations) are of very limited occurrence.

It is interesting to note that the disjunct Ontario population did not differ significantly from the western populations. However, this population did not contain either of the Luteolin glycosides characteristic of northern populations. It is also surprising that there are no systematic differences in flavonoid profiles between the four chromosome races.

Figure 11. Distribution of Luteolin 7-O- glucoside in populations of *A. cordifolia* surveyed: (●) present, (▲) absent; and approximate maximum extent of Wisconsin glaciation in North America (Geol. Surv. Can., 1968; Coulter *et al* , 1962).



Arnica latifolia - A total of 9 flavonoids (6 glycosides and 3 aglycones) were found in the 26 populations of *A. latifolia* surveyed (Table 10). Quercetin Gentiobioside and Viscosin were ubiquitous, Quercetin 3-0-glucoside (12 populations) and Kaempferol 3-0-glucoside (10 populations) were relatively common and randomly distributed and Apigenin 6-methyl ether was present in half the populations. In general, Apigenin 6-methyl ether is present in populations from the Rocky Mountains and absent in populations of the Pacific Northwest. Kaempferol 3-0-galactoside, which is otherwise rare in *Austromontana*, is both common (17 populations) and randomly distributed in *A. latifolia*. Another significant feature of its flavonoid profile is the replacement of Kaempferol 6-methyl ether-3-0-glucoside by Quercetin 6-methyl ether-3-0-glucoside in this taxon. Also of importance is the occurrence of the free aglyconesKaempferol and Quercetin 6-methyl ether in two populations of the Klamath Region of California.

A striking feature of the Alaskan population sampled is that only compounds based on Quercetin are present. Like *A. cordifolia*, no correlation between flavonoid profiles and ploidy level was noted. Also as in *A. cordifolia*, some populations of *A. latifolia* exhibit very depauperate flavonoid profiles.

Arnica gracilis - Although only 2 populations of *A. gracilis* were available for flavonoid analysis, its flavonoid profile is proving to be one of the most diverse, complex and systematically significant of all *Austromontana* species examined. Straley (1980)

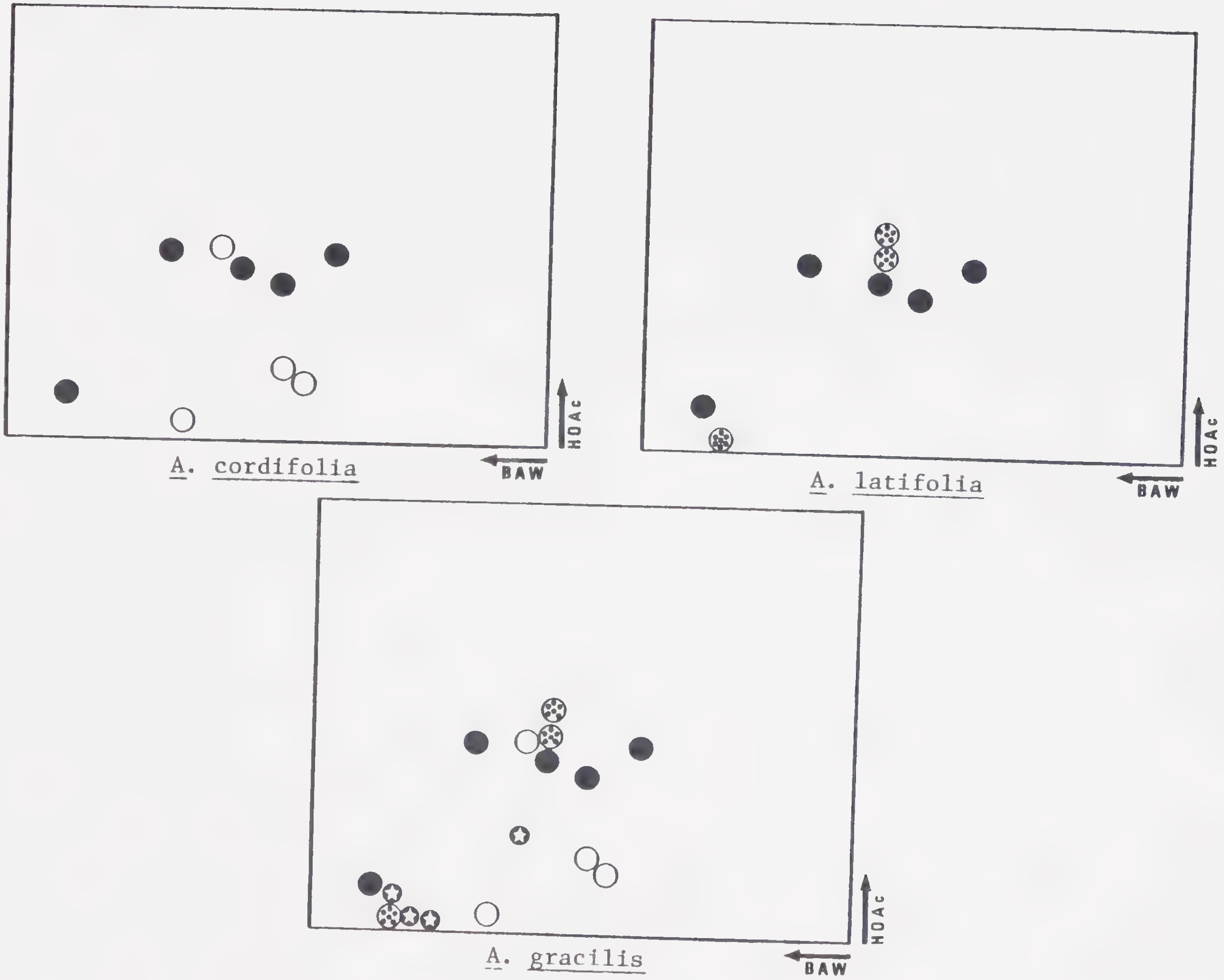
Table 10. Distribution of flavonoids in _A. latifolia_ populations surveyed.*

Location	Chromosome number (2n)	Collection number	A 6-Me	Q 6-Me	Kaempferol	Q-Gentiobioside	Viscosin	Q 6Me, 3-O-glu	Q 3-O-glu	K 3-O-glu	K 3-O-gal
AK	38	W503				+	+	+	+		
ALT	38	W321	+			+	+	+			
ALT	38	W319				+	+	+	+		
ALT	38	W513				+	+		+	+	+
ALT	76	D7830				+	+				
CA	76	W465		+	+	+	+				+
CA	76	W467		+	+	+	+	+	+	+	+
CO	38	W416	+			+	+	+	+		+
ID	38	W357	+			+	+	+			+
ID	38	W352	+			+	+			+	+
ID	76	W490	+			+	+	+			+
ID	76	W360	+			+	+	+			
ID	76	W488	+			+	+	+	+	+	
MT	38	W344	+			+	+	+	+		+
MT	76	W494				+	+				
MT	76	W489	+			+	+				+
MT	76	W436	+			+	+	+			+
OR	38	W379				+	+	+	+	+	+
OR	38	W380				+	+	+			+
OR	38	W457		+		+	+				
UT	38	W397	+			+	+	+	+	+	+
WA	38	W376				+	+	+	+	+	+
WA	38	W372				+	+	+		+	+
WA	38	W369				+	+			+	
WY	38	W424	+			+	+	+	+		+
WY	38	W431	+			+	+	+	+		+

*Abbreviations: A-Apigenin, Q-Quercetin, K-Kaempferol, Me-methoxyl, glu-glucoside, gal-galactoside.

suggested that this species might be a hybrid between *A. latifolia* and some other species. Results of the present investigation support this conclusion. *Arnica gracilis* appears to be a hybrid between *A. latifolia* and *A. cordifolia*.

Harborne (1975) noted that the flavonoid profiles of hybrids are frequently a summation of the two parental flavonoid profiles; however, novel flavonoids, i.e. those present in neither of the parents, occasionally appear in the hybrids (cf. Levy and Levin, 1971). A total of 16 flavonoids have been characterized from the 2 populations of *A. gracilis* examined (Table 8). A 2-dimensional chromatogram of the flavonoids of *A. gracilis* and its presumed parents *A. cordifolia* and *A. latifolia* are presented in Figure 12. Of the 16 compounds found in *A. gracilis*, 5 occur in both *A. latifolia* and *A. cordifolia* (Apigenin 6-methyl ether, Kaempferol 3-0-glucoside, Quercetin 3-0-glucoside, Viscosin and Quercetin Gentiobioside, 3 are found in *A. latifolia* (Quercetin 6-methyl ether, Quercetin 6-methyl ether-3-0-glucoside and Kaempferol 3-0-galactoside), 3 are found in *A. cordifolia* (Luteolin 7-0-glucoside, Luteolin 6-methyl ether-7-0-glucoside and Quercetin 3 methyl ether) and the 4 novel compounds (Luteolin, Luteolin 6-methyl ether, Luteolin 4'-methyl ether and Apigenin 7-0-glucoside) occur in neither of these 2 species. Of the two populations surveyed *S. Wolf 350*, ALTA (from Idaho) contained all but one of these 16 compounds while *S. Wolf 324*, ALT (from Alberta) was deficient in several glycosides and contained only 9 compounds. The distribution of



A. cordifolia

A. latifolia

A. gracilis

Figure 12. 2-Dimensional chromatograms of A. cordifolia, A. latifolia and A. gracilis.

these compounds in the 2 populations is presented below.

Compound	W324	W350
Apigenin 6-methyl ether	-	+
Luteolin	-	+
Luteolin 6-methyl ether	+	+
Luteolin 4'-methyl ether	-	+
Quercetin 3-methyl ether	+	+
Quercetin 6-methyl ether	+	+
Apigenin 7-0-glucoside	+	+
Luteolin 7-0-glucoside	+	+
Luteolin 6-Me-7-0-glu	-	+
Kaempferol 3-0-glucoside	-	+
Kaempferol 3-0-galactoside	+	+
Kaempferol 6-Me-3-0-glu	+	-
Quercetin 3-0-glucoside	+	+
Viscosin	-	+
Quercetin Gentiobioside	-	+
Quercetin 6-Me-3-0-glu	+	+
Total	9	15

The compound Kaempferol 3-0-galactoside, generally restricted to A. latifolia, and Quercetin 6-methyl ether and its 3-0-glucoside establishes a clear relationship between A. gracilis and A. latifolia. As previsouly noted, A. gracilis has at times been treated as a subspecies of A. latifolia. The compounds Luteolin 7-0-glucoside, Luteolin 6-methyl ether-0-glucoside and Quercertin 3-methyl ether clearly establish a relationship between A. gracilis and A. cordifolia. The occurrence of Luteolin and its 6-methyl ether in A. gracilis is not surprising since glycosides of these compounds also occur in A. cordifolia. The presence of Luteolin 4'-methyl ether in both A. gracilis and A. nevadensis is somewhat anomalous; however, as will be discussed subsequently, A. nevadensis is very closely related to and probably derived from A.

cordifolia. The most diagnostic compound in *A. gracilis* is Apigenin 7-0-glucoside. Neither this compound nor any other glycosides of Apigenin have been found in any other *Austromontana* species.

Arnica discoidea - A total of 12 flavonoids (7 glycosides and 5 aglycones) were found in the 11 populations of *A. discoidea* surveyed (Table 11). Quercetin Gentiobioside, Viscosin and Kaempferol 3-0-glucoside were ubiquitous; Apigenin 6-methyl ether was found in 10 populations and Quercetin 3-0-glucoside was present in 9 populations. Two significant aspects of the flavonoid profile of this species are readily apparent, (1) populations of the Klamath region dffer significantly from those of other areas, (2) the species profile shows strong affinity with that of *A. cordifolia*. Luteolin 6,4 di-methyl ether (3 populations), Luteolin 7-0-glucoside (3 populations) and Luteolin 6-methyl ether-7-0-glucoside (2 populations) are restricted to populations of the Klamath region. In addition, the latter 2 compounds are found elsewhere only in northern populations of *A. cordifolia* and its derivative *A. gracilis*. Further, the presence of Kaempferol 6-methyl ether-3-0-glucoside and Apigenin 7-methyl ether in *A. discoidea* suggests a close relationship to *A. cordifolia*. As previously noted, Apigenin 7-methyl ether has been found in one population of *A. cordifolia* from California. Results of the present investigation support Maguire's (1943) and Straley's (1980) hypotheses that *A. discoidea* is probably derived from *A. cordifolia*.

Table 11. Distribution of flavonoids in _A. discoidea_ and _A. spathulata_ populations surveyed.*

	Location	Chromosome numbers (2n)	Collection number	Apigenin	A 6-Me	A 7-Me	A 6, 7-Me	L 6, 4'-diMe	Q-Gentiobioside	Viscosin	K 6-Me, 3-O-glu	Q 3-O-glu	K 3-O-glu	L 6-Me, 7-O-glu	L 7-O-glu
A. discoidea															
	CA	38	W470	+	+		+	+	+	+	+	+	+		
	CA	38	W390		+			+	+	+		+	+	+	+
	CA	38	W389					+	+	+		+	+		+
	CA	38	W466		+	+	+		+	+	+	+	+	+	+
	CA	38	W472		+	+			+	+			+		
	CA	38	W475	+	+	+	+		+	+	+	+	+		
	CA	38	W474	+	+				+	+	+	+	+		
	CA	57	W477		+		+		+	+	+	+	+		
	CA	76	W392		+		+		+	+	+	+	+		
	CA	76	W473	+	+		+		+	+	+	+	+		
	CA	?	W515		+	+			+	+	+		+		
A. spathulata															
	CA	38	W458		+	+			+	+	+	+	+		
	CA	76	W459						+	+	+				
	OR	38	W455		+			+	+	+	+	+	+		
	OR	38	W456		+			+	+	+	+	+	+		
	OR	38	W462		+			+	+	+	+		+		
	OR	38	W463		+			+	+	+	+		+		
	OR	38	W384		+				+	+	+		+		
	OR	38	W460						+	+	+				
	OR	76	W461						+	+	+				

*Abbreviations: A-Apigenin, L-Luteolin, Q-Quercetin, K-Kaempferol, Me-methoxyl, glu-glucoside.

As in other *Austromontana* species, no differences in flavonoid profiles were noted with respect to the 3 chromosome races of *A. discoidea*. In addition, an attempt was made to compare the flavonoid profiles of the 3 infraspecific taxa (of *A. discoidea*) previously recognized by Maguire (1943) and Ediger and Barkely (1978). No differences were noted, supporting the treatment of this taxon as a single polymorphic species.

Arnica spathulata - A total of 8 flavonoids (5 glycosides and 3 aglycones) were found in the 9 populations of *A. spathulata* sampled (Table 11). The flavonoid profile of this taxon is basically a subset of *A. discoidea*. Quercetin Gentiobioside, Viscosin and Kaempferol 6-methyl ether-3-0-glucoside were ubiquitous; the 3-0-glucosides of Quercetin (3 populations) and Kaempferol (6 populations) were randomly distributed and Apigenin 6-methyl ether was present in 6 populations. Like *A. discoidea* this taxon contains both Apigenin 7-methyl ether (1 population) and Luteolin 6,4' di-methyl ether (4 populations). As previously noted, the latter compound was present only in populations of *A. discoidea* from the Klamath region. It is significant to note that *A. spathulata* is a rare endemic of the Klamath region and it has previously been suggested that this taxon is a derivative of *A. discoidea* (Maguire, 1943). Results of the present investigation support this observation.

No correlations between flavonoid profiles and ploidy level were noted in *A. spathulata*. In addition, populations which have

been previously treated as ssp. *eastwoodiae* because of their purple colour and/or narrower leaves (Maguire, 1943) were not distinguishable based on flavonoid profiles.

Arnica venosa - Two populations of this rare species were sampled for flavonoid content (Table 8). A total of 6 compounds including the 4 glycosides: Quercetin Gentiobioside, Viscosin, Kaempferol 3-O-glucoside and Kaempferol 6-methyl ether 3-O-glucoside; and 2 aglycones Apigenin 6 and 7 methyl ethers were found in both populations. Like *A. spathulata* this taxon exhibits a subset of the *A. discoidea* flavonoid profile. Prior to the present investigation too few specimens of *A. venosa* were available to support any hypotheses about its possible relationships. In the present study this taxon is treated as a recent derivative of *A. discoidea*. The similar flavonoid profiles of *A. discoidea* and *A. venosa* (as well as evidence to be presented elsewhere) supports this view. The depauperate flavonoid profile of the latter may be the result of genetic depletion in this rare species.

Arnica nevadensis - Only 2 populations of *A. nevadensis* were available for flavonoid analysis. A total of 6 compounds including the glycosides Quercetin 3-O-glucoside, Viscosin and Quercetin Gentiobioside and aglycones Apigenin 6-methyl ether, Luteolin 6-methyl ether and Luteolin 4'-methyl ether were found in both populations examined (Table 8). As previously noted, the latter 2 compounds are also present in *A. gracilis*. Few systematic conclusions about *A. nevadensis* can be made based on its flavonoid pro-

file. Luteolin 6-methyl ether provides a possible link between *A. nevadensis* and *A. cordifolia* since the 3-0-glucoside of this compound occurs in the latter. Also, as previously noted, *A. gracilis* is probably derived from *A. cordifolia*.

Arnica cernua - Two populations of this rare serpentine endemic of the Klamath region were examined for flavonoid content. The flavonoid profile of this taxon supports the hypothesis of genetic depletion in rare species put forth by Stebbins (1980). Both populations contained only 3 flavonoids: Kaempferol 3-0-glucoside, Quercetin Gentiobioside and Viscosin; all of which are of common occurrence in *Austromontana*. Therefore, no systematic conclusions can be made based on the flavonoid profile of this taxon. However, since the 2 populations sampled were geographically well separated, it might be reasonable to assume that the depauperate flavonoid profile represents the ancestral condition in *A. cernua* which became established prior to dispersal of this taxon. It seems unlikely that these 2 isolated populations would otherwise have identical flavonoid profiles.

Arnica viscosa - Although only 2 populations of this rare species were sampled for flavonoid content, its flavonoid profile has proven to be the most complex and diverse of all *Austromontana* species. A total of 15 flavonoids, including 7 glycosides and 8 aglycones were found in both populations (Table 8). The flavonoid profile of this taxon runs the entire gamut from simple flavonols and flavones through simple methyl ethers to highly complex methyl

ethers. In addition to showing affinities to several taxa, the flavonoid profile of this species contains several compounds not found in any other Austromontana species. The flavonoids Apigenin 6-methyl ether, Kaempferol 3-0-glucoside, Quercetin 3-0-glucoside, Visosin and Quercetin Gentiobioside are found throughout the subgenus. Compounds common to both A. viscosa and A. discoidea (or its derivatives) include Apigenin, Apigenin 7-methyl ether, Apigenin 6,7-di-methyl ether and Luteolin 6,4'-di-methyl ether. Quercetin 6-methyl ether-3-0-glucoside is found elsewhere only in A. latifolia and its derivative A. gracilis. The aglycones Luteolin 3,6,7-tri-methyl ether, Luteolin 6-hydroxy-4'-methyl ether and Quercetin 3',6-di-methyl ether are unique to A. viscosa. In addition, two di- or tri-glycosides are unique to this taxon. Due to insufficient material, no aglycone analysis could be made of these compounds, and so they are designated as A. viscosa numbers 10 and 11 (chromatographic and spectral properites are given in Table 7).

Harborne (1977) has summarized the flavonoid chemistry of the Compositae. A typical flavonoid profile may contain flavonols, flavones or C-glycosylflavones; however, when the latter are present one of the former is almost always absent. The subgenus Austromontana is therefore unusual since it contains both flavones and flavonols while lacking C-glycosylflavones. In general, the family is noted for containing many highly methylated compounds with simple methyl ethers, such as Quercetin 6-methyl ether and Apigenin 6-methyl ether not uncommon. Another significant feature

of the family is its general lack of glycoside variability. Few glycosyl sugars other than glucose and rhamnose (often combined in rutinosides) occur in the family. As Harborne (1977) noted, glycoside variability within the family has largely been replaced by glycoside complexity, i.e. unusual sugar linkages. The low glycoside variability in Austromontana as well as the unusual sugar linkages of the di-glucosides Quercetin Gentiobioside and Viscosin conform to this pattern.

Flavonoids have been used extensively in systematic studies of the Compositae. In a study of the Coreopsis mutica complex, Crawford (1970) found significant correlations between chromosome number, geographical distribution and flavonoid chemistry. In a study of 44 populations of the Senecio radicans complex, with chromosome numbers ranging from 2n = 20 - 180, Glennie et al (1971) found no correlations between flavonoid profile and chromosome number. However, the authors demonstrated that dispersal from ancestral areas was accompanied by reductions in flavonoid diversity. Mabry et al (1975) showed a similar reduction concomitant with range expansion in Veronia. In Tripleurospermum and Matricaria Greger (1975) noted the replacement of flavonols and their simple methyl ethers in primitive taxa by highly methylated flavones and 6-hydroxy-Luteolin in advanced taxa. Finally, in a study of Tragopogon hybrids, Brehm and Ownbey (1965) found that flavonoid profiles revealed more about hybridization than was morphologically apparent.

Several significant features of the flavonoid chemistry of Austromontana are readily apparent. Several compounds are present in all taxa (e.g., Viscosin and Quercetin Gentiobioside) while some are restricted to a few or even only one taxon (e.g., Apigenin 7-0-glucoside and Luteolin 6OH-4'-methyl ether), certain compounds such as Luteolin 7-0-glucoside and Luteolin 6-Me-7-0-glucoside indicate phylogenetic relationships and the distribution of some compounds (e.g., Quercetin 3-0-glucoside and Kaempferol 3-0-glucoside) appears to be random while others have significant geographical correlations. As Harborne (1975) noted, the utility of flavonoid data often varies greatly depending on the taxa investigated. For example, all 17 species of Baptisia (Leguminosae) examined by Markham et al (1970) could be identified by their flavonoid pattern. In contrast, all 11 species of Thelesperma (Compositae) examined by Melchert (1966) had the same flavonoid profile. As in most taxa, the situation in Austromontana lies somewhere between these two extremes.

Such flavonoids as: Quercetin Gentiobioside, Viscosin and Apigenin 6-methyl ether are virtually ubiquitous in Austromontana, indicating a close relationship between all species in the subgenus. Such compounds as Quercetin 3-0-glucoside and Kaempferol 3-0-glucoside, although common, have been reported in several other Arnica species, suggesting that they may represent an ancestral condition in the genus. At the other extreme, compounds unique to only one species, as in A. viscosa, indicate considerable divergence from the ancestral condition.

The analysis of the flavonoid chemistry of *Austromontana* has proven most useful in deducing new or confirming previously proposed evolutionary relationships. The flavonoid profile of *A. gracilis* alone is prima facie evidence of its hybrid derivation from *A. cordifolia* and *A. latifolia*. The profile of this taxon is essentially a summation of the two parental profiles. The presence of Luteolin 6-methyl ether-7-0-glucoside and Luteolin 7-0-glucoside in both *A. cordifolia* and *A. discoidea* supports Maguire's (1943) hypothesis that the latter is derived from the former. Maguire (1943) also hypothesized that the Klamath endemic *A. spathulata* was derived from *A. discoidea*. The similar flavonoid profiles of these 2 taxa and the presence of Luteolin 6,4'-methyl ether (common to both species) only in Klamath populations of *A. discoidea* supports this hypothesis. In addition, the presence of Kaempferol 6-methyl ether-3-0-glucoside, among other compounds, in both *A. discoidea* and *A. venosa* suggests the latter is derived from the former.

A further aspect of the chemistry of the taxa in *Austromontana* is the concomitant reduction of flavonoid diversity with narrowness in geographical distribution. With the exception of *A. viscosa*, the rarer the taxon, the fewer compounds it contains. A striking example of this occurs in *A. discoidea* and its rare derivatives *A. spathulata* and *A. venosa*. Another example is *A. cernua*, a rare serpentine endemic, that contains only 3 compounds. An example of another type of isolation, i.e. genetic, occurs in one of the rare

diploid populations of *A. cordifolia* (*S. Wolf 347*, ALTA). This population is essentially a diploid island in a sea of polyploids and exhibits a very depauperate flavonoid profile. This supports Barker's (1966) hypothesis of genetic depletion in rare isolated diploid populations of this taxon.

Harborne (1977) has discussed the evolution of flavonoids and their use in phylogenetic studies. According to him a primitive flavonoid profile would consist of only flavonols with no methylation and no hydroxylation at the 6-position. In contrast, the most advanced profile would consist of highly methylated flavones with 6-position hydroxylation. Crawford (1978), although agreeing with Harborne, noted that an evaluation of pleisiotypic versus apotypic profiles can only be made in conjunction with all available information. This is especially true in *Austromontana* since several taxa viewed as recently derived have very simple flavonoid profiles. The most plesiomorphic profile in the subgenus would appear to be *A. cernua* however, as previously noted, this is probably the result of genetic depletion. Based on Harborne's (1977) criteria, *A. cordifolia* and *A. latifolia* represent the ancestral condition in the subgenus. These two species contain predominantly flavonols and their simple methyl ethers. In contrast *A. viscosa* exhibits the most advanced flavonoid profile within the subgenus. This taxon elaborates a number of highly methylated flavones and exhibits the very advanced condition of hydroxylation at the 6-position. The divergence of *A. discoidea* from *A. cordifolia* has in-

volved an elaboration of highly methylated flavones, some of which have been secondarily lost in its derived rare species *A. spathulata* and *A. discoidea*.

The flavonoid profile of *Austromontana* indicates that evolutionary diversification within the subgenus, from the widespread *A. cordifolia* and *A. latifolia* has been accompanied by a general trend of increasing flavone production followed by methylation and 6-position hydroxylation. In addition, a secondary trend of reduction has occurred in some of the more recently derived rare taxa.

PHYLOGENY AND PHYTOGEOGRAPHY

Maguire (1943) considered the genus Arnica to have arisen in Arctic or sub-Arctic western North America from where it spread eastward, westward and southward. Hultén (1937) listed 22 species of Arnica (some of which were not recognized by Maguire, 1943) that are of probable northwest North American origin. The fact that most species of the genus are adapted to cool montane habitats and that 25 of the 32 species recognized by Maguire (1943) are largely confined to northwestern North America supports this conclusion. Additional evidence to support this hypothesis is the presence of many relictual diploid races, of otherwise widespread Arnica polyploid complexes, in the unglaciated Alaska-Yukon region (Wolf, 1980). Phytogeographical evidence suggests that the genus Arnica is relatively old, and was part of the Arcto Tertiary Flora. The east-west disjunct distribution of A. louiseana Farr and A. lonchophylla D.C. Eaton, the circumpolar distribution of A. angustifolia Vahl and the close relationship between A. montana of Europe and A. acaulis of the eastern United States lends support to this theory.

Raven and Axelrod (1978) included the genus Arnica within a group of genera that are well-developed in California, yet widespread elsewhere. They suggested that this recurrent pattern in the Californian flora is the result of spreading aridity from Upper Tertiary times in the western United States which culminated in the

development of a full mediterranean climate in the late Quaternary. A striking example of this distribution pattern occurs within subgenus *Austromontana* which contains both widespread species (e.g., *A. cordifolia* and *A. latifolia*) and several narrow endemics (e.g., *A. cernua*, *A. venosa* and *A. viscosa*). In fact, the discoid species of *Austromontana* are confined almost entirely to the northern areas of the California Floristic Province, particularly within the Klamath region of southwestern Oregon and northwestern California. The occurrence of many endemics in the Klamath region and its significance in the evolution and development of the flora of the western states, particularly California, has been discussed by Whittaker (1960, 1961). Due to its geological history, equable climate and diversity of parent soils, the Klamath region contains many endemics that probably represent both remnants of the Arcto Tertiary Flora and more recently derived taxa (Whittaker, 1961). In the case of subgenus *Austromontana*, the narrow endemics appear to be recently derived from the more widespread *A. cordifolia* and *A. latifolia*.

Maguire (1943) considered *A. cordifolia* to represent the ancestral species in *Austromontana* which gave rise to the rest of the subgenus. Results of the present investigation support this hypothesis. With respect to morphology, *A. cordifolia* exhibits virtually all features considered plesiomorphous within the genus *Arnica* in general and the subgenus *Austromontana* in particular. Morphological characters considered plesiomorphous and apomorphous

have previously been discussed and are summarized in Table 12,page 130. Significant plesiomorphous features of A. cordifolia include: solitary, broad heads with white, barbellate pappus; unbranched stems with few, narrowly petiolate, broad, dentate leaves and dark grey achenes. In addition, the flavonoid profile of A. cordifolia, which lacks complex methylation, is relatively plesiomorphous. Additionally, the mesic-montane habitat of A. cordifolia represents the ancestral condition within the genus Arnica in general (Maguire, 1943). Indeed, within Austromontana there is a distinct evolutionary trend from mesic-montane habitats towards drier habitats at both lower and higher elevations.

Phytogeographical, cytological and chemical evidence suggests that A. cordifolia was probably a relatively widespread diploid species prior to the Pleistocene. Hultén (1937) included A. cordifolia in a group of species widespread prior to the Pleistocene, but whose ranges were interrupted by glaciation. He hypothesized that these species survived the Pleistocene glaciations south of the ice, in the unglaciated areas of the Yukon and also possibly on mountain nunataks. Upon retreat of the ice, these populations were rejoined to form a continuous distribution. Chemical and cytological data support this hypothesis for A. cordifolia. Virtually all populations of A. cordifolia which occur north of the maximum limit of Pleistocene glaciation possess Luteolin 7-0-glucoside, while southern populations lack this compound. The presence of Luteolin 7-0-glucoside in A. chamissonis Lessing

(northwest North America), *A. sachalinensis* (Regl.) A. Gray (Siberia), *A. montana* (Europe) (Borkowski *et al*, 1966) and in northern populations of *A. cordifolia* suggest that this compound may represent an ancestral pre-Pleistocene condition within the genus.

The absence of Luteolin 7-0-glucoside in the Ontario population of *A. cordifolia* poses an interesting problem. Fernald (1925) considered the disjunct western cordilleran taxa of the upper Great Lakes region (such as *A. cordifolia*) to have survived the Pleistocene glaciations largely in the driftless area of Wisconsin. Hultén (1937) hypothesized a plant refugium in the upper Great Lakes region and/or the southern Hudson Bay region to account for this pattern of distribution. However, the lack of Luteolin 7-0-glucoside in the Ontario population suggests it is more closely related to the southern populations which lack this compound. Cushing (1965) proposed two explanations for the disjunct occurrence of Rocky Mountain taxa in the upper Great Lakes region. Either they are the result of long distance dispersal from the west or they are the result of the destruction of favorable intervening habitats that were occupied by these taxa in late-glacial or earlier post-glacial time. Weber (1965) noted that during the Pleistocene the Rocky Mountain flora extended far to the east and upon retreat westward, elements of this flora remained behind in more favorable habitats. The presence of *A. cordifolia* in the Black Hills of South Dakota and the Cypress Hills of Alberta and

Saskatchewan can best be explained in this way. The presence of *A. cordifolia* in the upper Great Lakes region as well as the Pasquia Hills of Saskatchewan and western Manitoba could also be the result of dispersal from this eastward extension of the Rocky Mountain flora.

Cytological evidence also supports the hypothesis that *A. cordifolia* was probably a relatively widespread diploid species prior to the Pleistocene. Barker (1966) hypothesized that within the genus *Arnica* diploids were more widespread in the past and that polyploidy in the genus is a relatively recent, i.e., inter or post-glacial phenomenon. Stebbins (1971) noted that most mature polyploid complexes such as *A. cordifolia* are of Pliocene or Pleistocene origin. The occurrence of diploid populations of *A. cordifolia* in the unglaciated Yukon as well as south of the limit of glaciation (in Oregon) suggests a former, much wider distribution of diploid populations. The fact that the Michigan populations of this species are tetraploid argues against their survival as pre-Pleistocene relicts. If they are in fact relicts, they might be expected to be diploid.

Without further cytological and chemical analysis of additional disjunct populations of *A. cordifolia*, the causes of their distribution must remain only speculative. However, the most plausible explanation appears to be a combination of Pleistocene eastward migration of the Rocky Mountain flora followed by post-Pleistocene "stranding" of populations in more favorable habitats.

Further eastward dispersal from these intervening populations may have also occurred, both during and immediately after the glacial epochs.

The geographical distribution, morphology, cytology and flavonoid chemistry of A. latifolia suggests that it is probably a pre-Pleistocene derivative of A. cordifolia. Arnica latifolia occurs throughout much of the range of A. cordifolia in moister habitats. at higher elevations. Morphologically the two species are very similar and are often difficult to distinguish on herbarium sheets. Arnica latifolia and A. cordifolia share several plesiomorphous characters including: radiate heads with white, barbellate pappus; relatively few, broad leaves; innovations and numerous, yellow disc florets. However, A. latifolia can readily be distinguished by its sessile leaves, narrow heads and phyllaries, and brown achenes.

Although the flavonoid profile of A. latifolia, like that of A. cordifolia is relatively plesiomorphous, the two species differ in several aspects. Most notable is the replacement of Kaempferol 6-methyl ether-3-0-glucoside in A. cordifolia by Quercetin 6-methyl ether-3-0-glucoside in A. latifolia. Additional differences between the two species include Luteolin 7-0-glucoside and Luteolin 6-methyl ether-7-0-glucoside in A. cordifolia and Kaempferol 3-0-galactoside in A. latifolia.

The largely diploid condition of A. latifolia suggests a pre-Pleistocene divergence from A. cordifolia prior to the elimina-

tion of the diploid level in the latter. Arnica latifolia may have been an ecological race of an archetypal "cordifolia" adapted to moister conditions, which became established after the advent of apomixis in the latter. The fact that A. cordifolia and A. latifolia probably hybridized and produced A. gracilis (see below) also suggests a close relationship between the two species.

As previously noted, there is little doubt that A. gracilis is the product of hybridization between A. latifolia and A. cordifolia. The close morphological relationship between A. latifolia and A. gracilis has long been noted (Maguire, 1943) and is reflected in the nomenclature of the latter (see Taxonomy section). However, ecologically the two species are well defined, with A. gracilis occupying exposed alpine rock outcrops and A. latifolia occurring in fairly moist sub-alpine meadows. Recently, Straley (1980) hypothesized that A. gracilis is the product of hybridization between A. latifolia and some other Arnica species. Considering the degree of sympatry frequently observed in many A. latifolia and A. cordifolia populations it would indeed be surprising if they never hybridize. For example, the population of A. gracilis (S. Wolf 324 ALTA) from Highwood Pass, Alberta was collected on a rock outcrop less than 3 meters above a large population of A. latifolia which was itself only a few meters above a large population of A. cordifolia. A very similar situation was also noted with respect to the other A. gracilis population collected in Idaho (S. Wolf 350 ALTA).

Arnica gracilis, with its relatively narrow, serrate, petiolate leaves and turbinate-campanulate heads is somewhat morphologically intermediate between *A. latifolia* and *A. cordifolia*. However, its branched habit, numerous heads with a reduced number of disc florets, and black achenes with glandular hairs represent derived states in the subgenus *Austromontana*.

As previously noted, the flavonoid profile of *A. gracilis* is essentially a summation of its presumed parents, *A. latifolia* and *A. cordifolia* (see Figure 12, page 8). Compounds common to both *A. gracilis* and *A. cordifolia* include: Quercetin 3-methyl ether, Luteolin 7-0-glucoside, Luteolin 6-methyl ether-7-0-glucoside and Kaempferol 6-methyl ether-3-0-glucoside. Compounds common to both *A. gracilis* and *A. latifolia* include: Kaempferol 3-0-galactoside, Quercetin 6-methyl ether and its 3-0-glucoside.

With the exception of southern Alberta and British Columbia, *A. gracilis* is restricted primarily to areas south of the maximum extent of Pleistocene glaciation. Barker (1966) suggested that apomixis and polyploidy in *Arnica* is probably of Pleistocene origin. It therefore seems likely that the formation of *A. gracilis* may have taken place in the central Rocky Mountains during the Pleistocene, prior to the establishment of apomixis in *A. cordifolia*. The diversification and establishment of the hybrid product was probably facilitated by its ecological and subsequent genetic isolation (via apomixis) from the parental species. The existence of both triploid and tetraploid races in *A. gracilis*

suggests that allopolyploidy and/or introgression may have been involved in its formation. Indeed, subsequent back-crossing with A. latifolia may account for the lack of morphological similarity between A. gracilis and A. cordifolia.

As previously noted, there seems to be little doubt that A. discoidea has been derived from A. cordifolia. Morphologically the two species are quite similar, almost to the extent that A. discoidea appears to be little more than a rayless A. cordifolia. However, A. discoidea is easily distinguished by several apomorphous features including: more numerous, narrower, discoid heads with a barbellate to subplumose pappus; more numerous, narrower leaves and glandular achenes.

The Klamath region of southwestern Oregon and adjacent northwestern California has been a major center of evolutionary diversification and contains many endemics that represent both remnants of the Arcto Tertiary Flora and more recently derived taxa (Whittaker, 1961). According to Raven and Axelrod (1978) diversification within this region, from more widespread taxa, has taken place largely as a response to increasing aridity at the end of the Tertiary. Ecological, chemical and cytological evidence suggests that A. discoidea was probably derived, prior to the Pleistocene, from the more widespread A. cordifolia.

Ecologically, A. discoidea and A. cordifolia are quite distinct. Arnica cordifolia is adapted to cool, mesic, montane habitats and is generally quite rare west of the Cascades. In contrast, A. discoidea occurs in hotter and drier habitats west of the

Sierras and Cascades. In both instances where the two species have been observed in close association, in the Sierrian foothills (this study) and in the central Cascades (Straley, 1980), *A. cordifolia* had flowered and set seed well over a month prior to the flowering of *A. discoidea*. Such early flowering of *A. cordifolia* is no doubt a means to escape the relatively warm-dry summer conditions of these areas.

Flavonoid chemistry, in particular, suggests a Klamath region derivation of *A. discoidea* from the more widespread *A. cordifolia*. With the exception of a few highly methylated, derived compounds in *A. discoidea*, the flavonoid profiles of the two species are quite similar (see Table 8). Of particular significance is the presence of Luteolin 7-0-glucoside (3 populations) and Luteolin 6-methyl ether-7-0-glucoside (2 populations) in Klamath populations of *A. discoidea*. As previously noted, these two compounds probably represent an ancestral pre-Pleistocene condition in *A. cordifolia* and are now restricted to northern populations of this taxon. This suggests that *A. discoidea* was derived from Klamath populations of *A. cordifolia* prior to the Pleistocene elimination of these two compounds in the latter. Subsequent dispersal of *A. discoidea* from this region may account for the loss of these compounds.

As previously noted, *A. cordifolia* was probably a widespread diploid species prior to the Pleistocene. Therefore, the derivation of diploid races of *A. discoidea* must have taken place prior

to the advent of polyploidy in *A. cordifolia*. Since the polyploid populations of *A. discoidea* occur largely at the extremes of its distribution (see Cytology section), subsequent dispersal of this taxon from its area of origin may have been accompanied and/or facilitated by polyploidization. Since *A. discoidea* is largely diploid, morphologically similar to *A. cordifolia* and shares two unique flavonoids with the latter, it seems likely that *A. discoidea* diverged from ancient diploid populations of *A. cordifolia* that were apparently more widespread prior to the Pleistocene. This divergence probably took place in the Klamath region, largely as a response to increasing aridity at the end of the Tertiary.

Results of the present investigation indicate that the Klamath region serpentine endemic *A. spathulata* has probably been derived from *A. discoidea*. Morphologically the two species are very similar, differing largely in leaf and petiole shape and degree of pubescence (Table 4, page 37). However, *A. spathulata* is readily distinguished by several derived features including: narrow phyllaries; narrower, broadly petiolate leaves and black achenes. Ecological distinctions between the two species are also readily apparent. *Arnica spathulata* occurs at lower elevations and in drier habitats on serpentine soils.

As previously noted, the flavonoid profile of *A. spathulata* is a subset of *A. discoidea* flavonoids (Table 8, page 72). However, the presence of Luteolin 6,4'di-methyl ether (which is common in *A.*

spathulata) in Klamath region populations of *A. discoidea* establishes a clear link between the two species.

Whittaker (1961) noted that the diversity of soil types in the Klamath region has contributed greatly to the formation of many local endemics. Kruckeberg (1954, 1969) suggested that serpentine endemism results from an adaptation to serpentine followed by biotype depletion and the development of isolated populations into local endemics. Lewis (1962) notes that many serpentine endemics originate by saltation speciation in marginal populations. As Raven and Axelrod (1978) note, marginal populations often occur on edaphic situations that are unique for the species as a whole. What these ideas suggest is that *A. spathulata* may have initially diverged from marginal populations of *A. discoidea* that gradually adapted to, and later became restricted to serpentine soils. The subsequent restriction of these populations to local isolated areas may have resulted in a gradual depletion of their flavonoid profiles. The fact that *A. discoidea* and *A. spathulata* are still morphologically somewhat similar suggests a fairly recent derivation of the latter. Indeed, Raven and Axelrod (1978) suggest that most herbaceous, localized serpentine endemics of the California Floristic Province (such as *A. spathulata*) originated in late Pleistocene or more recent time.

Until recently, *A. venosa* was known from only a few small populations which appeared to exhibit very little morphological variability (Straley, 1980). However, the recent discovery and

study of many new populations of this taxon has revealed that it, like other *Austromontana* species is quite variable, and intergrades with *A. discoidea*. Typical populations of *A. venosa* differ from *A. discoidea* in several apomorphous features including: numerous sessile leaves, woody caudex and a lack of innovations (Table 4, page 37). *Arnica venosa* is also distinguished by its strongly reticulate-veined leaves, more leafy and branched habit and preference for hotter, drier disturbed habitats. However, some specimens of *A. venosa* with thin, slightly woody rhizomes and few broadly petiolate, weakly veined leaves tend to resemble *A. discoidea* (see Taxonomy section). In addition, most species of *Austromontana* are characteristically more leafy and branched when they occur in open or disturbed habitats.

Arnica venosa is diploid and exhibits a very depauperate *A. discoidea* flavonoid profile. However, the presence of Apigenin 7-methyl ether in both species suggests they are related. Since *A. venosa* and *A. discoidea* occur sympatrically, have several flavonoids in common and are sometimes morphologically similar, it seems likely that the former is derived from the latter. *Arnica venosa* is restricted to the foothills of Shasta County, California in the hottest and driest habitat of any *Arnica* species known. This represents considerable divergence from the ancestral cool-montane habitat characteristic of the genus *Arnica*. The very localized distribution of *A. venosa*, its preference for recently disturbed habitats and derived ecology suggest it is very recently derived,

possibly during the post-glacial hypsithermal of 9,000 to 2,600 years ago (Flint, 1957).

As previously noted, the flavonoid profile of *A. cernua* is very depauperate and provides few clues to its evolutionary history. Since it lacks both flavones and methyl ethers, it most closely resembles *A. cordifolia* and *A. latifolia*. Indeed, *A. cernua* shows morphological affinities to both of these taxa. However, since *A. cernua* is diploid and exhibits normal bivalent pairing during meiosis, a hybrid origin seems unlikely. Both Maguire (1943) and Straley (1980) consider this rare serpentine endemic to be derived from *A. latifolia*. However, both *A. cernua* and *A. cordifolia* share several pleisomorphous morphological features including: long, narrow petioles; broad solitary heads with pilose and glandular, ovate-lanceolate phyllaries and dark grey achenes. In contrast, *A. latifolia* has sessile leaves; several narrow heads with lanceolate, sparsely pubescent phyllaries and brown achenes.

Raven and Axelrod (1978) suggested that *A. cernua* probably evolved from a more widespread species, in late Pleistocene or recent time via saltation speciation in marginal populations that gradually became adapted to and later restricted to serpentine soils. It seems likely that *A. cernua* has been derived from the more widespread *A. cordifolia* prior to the elimination of the diploid condition in the latter. The very depauperate flavonoid profile of *A. cernua* supports Kruckeberg's (1969) hypothesis of biotype depletion in localized edaphic endemics.

There seems to be little doubt that *A. nevadensis* has, at least in part, been derived from *A. cordifolia*. *Arnica nevadensis* is an extremely variable species which sometimes resembles little more than a high altitude ecotype of *A. cordifolia*. In fact, in the past, many high altitude Rocky Mountain populations of *A. cordifolia* have been erroneously identified as *A. nevadensis*. *Arnica cordifolia* and *A. nevadensis* share several plesiomorphous features including: solitary, radiate heads and simple stems with few, relatively broad leaves. However, the latter is readily distinguished by its often tawny, subplumose pappus, entire leaves, oblanceolate phyllaries and relatively high altitude, exposed habitat.

The flavonoid profile of *A. nevadensis*, although somewhat anomalous, bears some resemblance to *A. cordifolia*. The extreme morphological variability of *A. nevadensis*, its tetraploid condition, apomictic reproductive system and resemblance to *A. cordifolia* suggests either it is the result of introgression between the latter and another *Arnica* species or it is a high altitude microspecies of *A. cordifolia* that has become established and more widespread via apomictic reproduction. The evolution of *A. nevadensis* may have been facilitated by the climatic cooling of the late Pliocene or Pleistocene and/or saltation speciation of high altitude populations of *A. cordifolia*.

Arnica viscosa is one of the rarest and most distinctive species of the genus *Arnica*. It is known from about 7 populations

on high alpine volcanic slopes, largely in the Klamath region of Oregon and California. Its opposite leaves and chromosome number of *n* = 19, among other features, clearly places it within the genus and its pappus characters, broad leaves and flavonoid profile warrants its inclusion in the subgenus *Austromontana*. *Arnica viscosa* exhibits virtually every apomorphous morphological, ecological and chemical feature of both the genus *Arnica* and subgenus *Austromontana* (Table 12). Significant derived morphological features include: numerous, narrow, discoid heads with a reduced number of cream colored florets; highly branched habit; numerous, sessile, entire leaves; woody caudex and a lack of innovations. Its restriction to volcanic soils and dry, alpine habitat are also considered derived features. Additionally, the flavonoid profile of *A. viscosa*, which includes several highly methylated flavones and a 6-hydroxylated flavone, is considered highly apomorphous.

The very distinctive morphology, ecology and flavonoid chemistry of *A. viscosa* as well as its restriction to very recent habitats makes an evaluation of its evolutionary history quite difficult and highly speculative at best. Localized endemics with very distinctive morphologies are generally considered quite old and remnants of a once more widespread distribution (Raven and Axelrod, 1978). However, the similar advanced flavonoid profiles of the two populations of *A. viscosa* surveyed as well as the fact that virtually no interpopulational morphological variability is apparent between the widely scattered populations, suggest a recent

derivation. In addition, the habitats of these populations are all very recent, i.e., within the last 15,000 years (McKee, 1972; Norris and Webb, 1976). Indeed, the eruption of Mt. Mazama, and subsequent formaton of Crater Lake occurred about 7,000 years ago (McKee, 1972).

Lewis (1962) has proposed a mode of rapid evolution which might account for the derivation of _A_. _viscosa_. According to Lewis, this mode of speciation, termed catastrophic selection, can occur in marginal populations under extreme selection pressure and a concomitant severe reduction in population size. Catastrophic selection permits the survival of unique genotypes by producing immediate spatial isolation of the survivors, via elimination of the parental populations. Raven (1964) considers this mode of selection important in the formation of edaphic endemics.

Volcanic activity in the Pacific Northwest has occurred throughout most of the Cenozoic (McKee, 1972) and in the Klamath region since at least the Eocene (Whittaker, 1961). _Arnica_ _viscosa_ may be the result of catastrophic selection from a more widespread Pliocene or Pleistocene "protoviscosa" that became isolated due to volcanism, mountain building or glaciation. This precursor may have already been adapted to volcanic soils or selection for this habitat may have accompanied its isolation. This mode of speciation could account for the distinctive apomorphous morphology and flavonoid profile of _A_. _viscosa_. The present distribution of _A_. _viscosa_ on very recent substrates could be the result of subsequent

dispersal via wind and/or birds. Indeed, the persistent pappus of *Arnica* achenes makes them easily dispersed by winds. Additionally, the sticky, glandular achenes of *A. viscosa* would make them suitable for bird dispersal.

Maguire (1943) noted the similar leafy, branching habit and rootstock shared by *A. viscosa* and *A. venosa* and suggested they might be related. Straley (1980) considered *A. viscosa* to be a recent derivative of *A. venosa* and erected the new subgenus *Calarnica* to encompass the two species. However, even Maguire (1943) noted that the two species differ significantly in several important characters (Table 4, page 37). In fact, except for the superficial similarity of habit shared by the two species, they bear little resemblance to each other. Although quite distinct, *A. viscosa* shares several features with *A. latifolia* including: very narrow heads with lanceolate bracts; sessile ovatish leaves; and similarly glandular achenes which lack duplex hairs. In addition, in exposed populations of *A. latifolia* it is not unusual to find a few highly branched plants which bear a striking resemblance to *A. viscosa*.

Although the flavonoid profile of *A. viscosa* is much more complex and diverse than *A. latifolia*, the presence of Quercetin 6-methyl ether-3-0-glucoside in both suggests a possible relationship between the two species. Harborne (1967) noted radical color changes in floral flavonoids caused by the simple addition of hydroxyl or methyl groups at certain positions, particularly the 6

position of the molecule. If the floral flavonoid profile of *A. viscosa* is as complex as its leaf profile then the distinctive cream colored florets of this taxon may not be as unusual as previously thought.

The derivation of *A. viscosa* from *A. venosa*, as suggested by Straley (1980) also seems highly unlikely since the two species probably represent the two greatest ecological extremes within both the genus *Arnica* and subgenus *Austromontana*. *Arnica venosa* occurs at the lowest elevations and occupies the hottest and driest habitat of any *Arnica* while *A. viscosa*, in contrast, is restricted to cold, high alpine habitats on volcanic soils. The derivation of *A. viscosa* from *A. latifolia*, a sub-alpine species, seems much more likely since it would require only a slight ecological shift. In addition, both *A. viscosa* and *A. latifolia* are diploid and occur sympatrically.

Additional evidence to suggest a possible relationship between *A. viscosa* and *A. latifolia* are the results of Straley's (1980) hybridization experiments. Crosses between the two species were relatively successful and evidently produced the most vigorous progeny. Since *A. viscosa* shares several morphological, cytological and chemical features with *A. latifolia* it seems most closely related to the latter. However, since *A. viscosa* is morphologically, chemically and ecologically distinct, yet is diploid with normal bivalent formation (thus ruling out hybridization), its origin via catastrophic selection seems most likely.

The proposed phylogenetic relationships of the various species of Austromontana may be summarized as follows. Arnica cordifolia; with its broad heads, cool-montane ecology, very diverse cytology, seemingly ancient flavonoid profile and wide geographical distribution; is almost certainly the ancestral species of the subgenus. Arnica latifolia with a morphology, distribution, ecology and flavonoid profile very similar to A. cordifolia is viewed as an early derivative of the latter. The derivation of A. gracilis via hybridization between A. latifolia and A. cordifolia seems almost certain. The sympatric distribution of the parent species as well as the additive flavonoid profile of the hybrid supports this conclusion.

The flavonoid profile of A. discoidea as well as its morphological resemblance to a rayless A. cordifolia clearly indicates a derivation from the latter. In addition, morphological, distributional and flavonoid data indicate that the two rare endemics A. spathulata and A. venosa are derived from A. discoidea. Morphological evidence clearly establishes that A. cordifolia has been involved, at least partially, in the evolution of A. nevadensis. The latter may represent either a distinct apomictic line of A. cordifolia or the product of introgression between A. cordifolia and another species.

The unique characters that distinguish the rare endemics A. cernua and A. viscosa also serve to obscure their evolutionary relationships. Since both taxa are sexual diploids and exhibit

normal bivalent pairing during meiosis, it seems unlikely that hybridization has played any role in their evolution. *Arnica cernua* is most likely derived from *A. cordifolia* since it shares several morphological features with that taxon. Although it is one of the most distinctive arnicas, *A. viscosa* appears to be most closely related to *A. latifolia* with respect to morphology, ecology and the presence of Quercetin 6-methyl ether-3-0-glucoside.

In an effort to further elucidate possible phenetic and phylogenetic relationships among the species of *Austromontana*, both cladistic and phenetic analyses were undertaken. Duncan *et al* (1980) have recently provided a comprehensive review and comparison of the various methods of phenetic and cladistic analysis. Phenetic methods summarize similarities and differences without a consideration of the number and sequences of character changes (Colless, 1967) while cladistic methods attempt to express similarities and differences with respect to the number and sequence of character changes that have occurred during evolution (Duncan *et al*, 1980). In the present study, the method of Whiffen and Bierner (1972) was used for phenetic analysis while the method of Wagner (1961) was chosen for cladistic analysis. The former was chosen because it requires a minimum of computations and provides a very detailed explanation of how to construct the resulting phenogram. The method of Wagner (1961) was chosen because, since its inception, it has remained the most widely used method of cladistic analysis in botanical systematics.

Although the method of Whiffen and Bierner (1972) is called "a quick method for computing Wagner trees," it is in fact a method of phenetic analysis since no assumptions of plesiomorphic and apomorphic conditions are made. The method is summarized as follows:

"1. List all characters to be used, with their two states.
2. Arbitrarily designate one state as 0 and the alternate state as 1; intermediate states may be designated as 0.5 if desired.
3. Draw up a table of designated states of each character for each taxon. Taxa showing both states of a given character may be given the designation 0.5 for that character, if desired.
4. Estimate the differences between each taxon and all others in turn as the sum over all characters of the absolute values of the differences between the states of a given character for the two given taxa. Put more simply, this is, in fact, the number of characters for which the two taxa exhibit different states.
5. Draw up a table of the differences between taxa as found in step 4.
6. Designate one taxon as the most primitive (ancestral).
7. From the table in 5, list the taxa in order of absolute difference from the taxon found in 6, starting with the least, and ending with the most, different.
8. Take the first taxon from the list in 7, and add it to the forming tree above the taxon found in 6, and connect the two with a line. Lines joining two taxa will be referred to as the pathway between the two taxa.
9. Take the next taxon from 7 and, using the table from 5, find which of the taxa already in the tree is most similar (least different), and connect the former by a new pathway to the pathway immediately below the taxon already in the tree. If, in the first part of this step, two taxa have the same absolute difference from the taxon found in 6, place first the one which is most closely related to any one of the taxa already in the tree.
10. For as long as there are taxa available from 7, repeat step 9." (Whiffen and Bierner, 1972).

Characters used in phenetic analysis are listed in Tables 13 and 14, character states for the nine species of Austromontana are given in Table 15 and the computed differences between the species are given in Table 16. In a slight modification of the above method one state has been designated 0 while the alternate state has been designated 2. This was to eliminate fractions due to the large number of intermediate states exhibited by the nine species. All morphological and ecological characters listed in Table 13 have previously been discussed. With the exception of Viscosin, Quercetin Gentiobioside, Apigenin, Luteolin and Kaempferol; all flavonoids of the subgenus have been used in phenetic analysis. The former 2 compounds were not included since they are ubiquitous, while the latter 3 were not used because free, non-methylated aglycones are generally products of glycosidic breakdown (Harborne, 1967).

A further modification of the phenetic analysis involved the weighting of chemical characters. Due to the large number of flavonoids relative to morphological and ecological features, the absence of intermediate states and the depletion of flavonoids in several species, the relative weight of flavonoid characters was reduced by designating the contrasting states as 0 and 1 rather than 0 and 2. Flavonoid depletions in particular, tended to obscure and distort relationships that were otherwise discernable by morphological and ecological features. A phenogram using equal weighting of chemical, morphological and ecological characters is presented, for comparative purposes in Figure 13.

Table 13. Morphological and ecological characters and states used in phenetic analysis of Arnica subgenus Austromontana

	State	
Character	0	2
1 Head: shape	campanulate	turbinate
2 number	1-3	> 7
3 type	radiate	discoid
4 Pappus: color	white	white-tawny
5 setae	barbellate	barb.-subplumose
6 Stem branching	-	+
7 Leaf position	below midstem	evenly distributed
8 Underground parts	rhizome	caudex
9 Innovations	+	-
10 Leaves: # pairs	2-4	> 6
11 margin	dentate	entire
12 shape	cordate	broadly lanceolate
13 petioles	narrow	sessile
14 Disc florets: #	> 50	< 25
15 color	yellow	cream
16 Phyllaries: shape	ovate-lanceolate	lanceolate
17 vestiture	gland.+non-gland.	glandular
18 Achene: color	dark grey	brown or black
19 glandular hairs	-	+
20 Ecology	mesic	dry
21 Substrate specificity	-	+

Table 14. Chemical characters and states used in phenetic analysis of *Arnica* subgenus *Austromontana*

Character		State 0	State 1
22	A 6-Me	-	+
23	A 7-Me	-	+
24	A 6,7-di Me	-	+
25	L 6-Me	-	+
26	L 4'-Me	-	+
27	L 6OH, 4'Me	-	+
28	L 6,4'-di Me	-	+
29	L 3,6,7-tri Me	-	+
30	Q 3-Me	-	+
31	Q 6-Me	-	+
32	Q 3', 6 di-Me	-	+
33	A 7-0-glu	-	+
34	L 7-0-glu	-	+
35	L 6-Me; 7-0-glu	-	+
36	K 3-0-glu	-	+
37	K 3-0-gal	-	+
38	K 6-me, 3-0-glu	-	+
39	Q 3-0-glu	-	+
40	Q 6-Me, 3-0-glu	-	+

41	*A. viscosa* #10	-	+
42	*A. viscosa* #11	-	+

*Abbreviations: A-Apigenin, L-Luteolin, Q-Quercetin, K-Kaempferol, Me-methoxyl, glu-glucoside, gal-galactoside.

Table 15. Phenetic character states for the species of *Arnica* subgenus *Austromontana*

Character State	cernua	cordifolia	discoidea	gracilis	latifolia	nevadensis	spathulata	venosa	viscosa
	Species								
1	1	0	1	1	2	1	1	1	2
2	0	0	1	2	1	0	1	1	2
3	0	0	2	0	0	0	2	2	2
4	0	0	0	0	0	2	0	0	2
5	2	0	2	0	0	2	0	0	2
6	0	0	1	2	0	0	1	1	2
7	0	0	0	0	0	0	0	2	2
8	0	0	0	0	0	0	0	2	2
9	0	0	0	0	0	0	0	2	2
10	0	0	1	0	0	0	1	2	2
11	1	0	1	1	1	2	0	1	2
12	0	0	2	2	0	0	1	1	1
13	0	0	0	0	2	0	1	2	2
14	1	0	1	2	0	1	1	1	2

15	0	0	0	0	0	0	0	0	2
16	0	0	0	0	2	1	1	0	2
17	0	0	0	2	0	2	1	0	2
18	0	0	0	2	2	0	2	0	0
19	0	1	2	2	1	2	2	0	0
20	1	0	1	2	0	1	1	2	2
21	2	0	0	0	0	0	2	0	2
22	0	1	1	1	1	1	1	1	1
23	0	1	1	0	0	0	1	1	1
24	0	0	1	0	0	0	0	0	1
25	0	0	0	1	0	1	0	0	0
26	0	0	0	1	0	1	0	0	0
27	0	0	0	0	0	0	0	0	1
28	0	0	1	0	0	0	1	0	1
29	0	0	0	0	0	0	0	0	1
30	0	1	0	1	0	0	0	0	0
31	0	0	0	1	1	0	0	0	0
32	0	0	0	0	0	0	0	0	1
33	0	0	0	1	0	0	0	0	0
34	0	1	1	1	0	0	0	0	0
35	0	1	1	1	0	0	0	0	0
36	1	1	1	1	1	0	1	1	1
37	0	0	0	1	1	0	0	0	0
38	0	1	1	1	0	0	1	1	0
39	0	1	1	1	1	1	1	1	1

40	0	0	0	1	1	0	0	0	1
41	0	0	0	0	0	0	0	0	1
42	0	0	0	0	0	0	0	0	1

Table 16. Computed differences between the species of *Arnica* subgenus *Austromontana*

	A	B	C	D	E	F	G	H	I
A	0	16	19	30	20	15	21	24	40
B		0	17	24	18	21	21	24	50
C			0	23	27	22	14	19	37
D				0	24	25	35	32	46
E					0	23	21	26	42
F						0	24	31	39
G							0	19	33
H								0	26
I									0

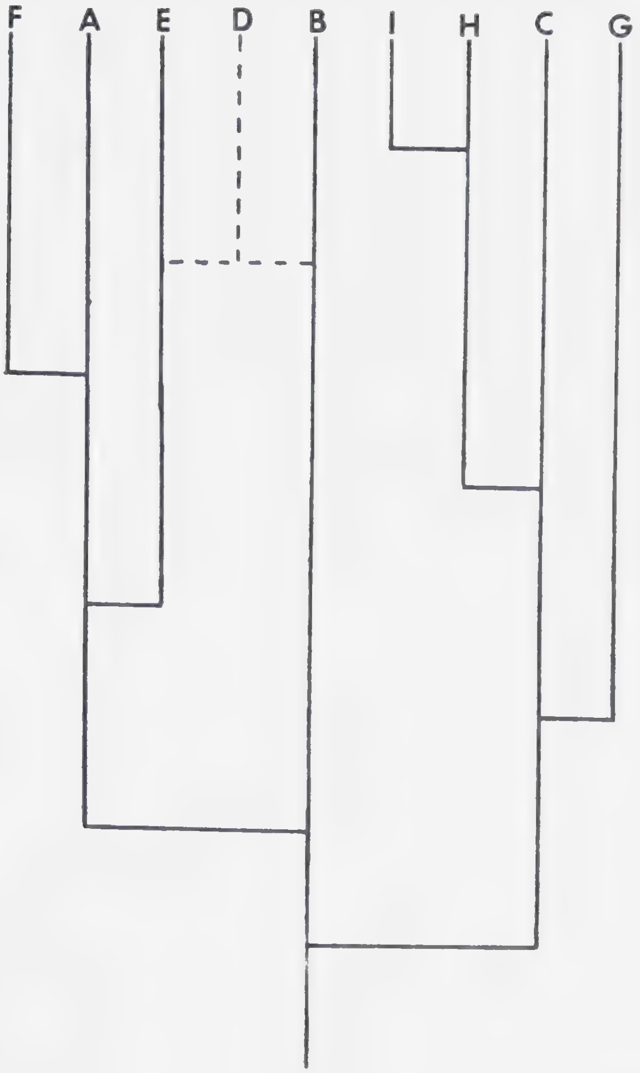


Figure 13. Phenetic relationships of the species of _Arnica_ subgenus _Austromontana_ using equal weighting of morphological, ecological and chemical characters. A- _A_. _cernua_, B- _A_. _cordifolia_, C- _A_. _discoidea_, D- _A_. _gracilis_, E- _A_. _latifolia_, F- _A_. _nevadensis_, G- _A_. _spathulata_, H- _A_. _venosa_, I- _A_. _viscosa_.

The phenogram produced by the method of Whiffen and Bierner (1972) using 0 and 2 for morphological and ecological states, 0 and 1 for flavonoid states and A. cordifolia as the "primitive" or starting point is presented in Figure 14. As previously noted, based on morphology, cytology, flavonoid chemistry and distribution; A. cordifolia most likely represents the ancestral species of the subgenus Austromontana. The only modification of the phenogram has been in the positioning of A. gracilis. Whiffen and Bierner (1972) suggest that modifications with respect to hybrid taxa may be necessary in some phenograms. In Figure 14, A. gracilis originally branched from A. discoidea based on a computed difference of 23 (Table 16). However, A. gracilis has been placed in a position intermediate between A. latifolia and A. cordifolia to reflect its hybrid status. Indeed, the computed differences between A. gracilis and both A. cordifolia and A. latifolia are 24 (Table 16), only one more than the 23 between the former and A. discoidea.

With the exception of the position of A. viscosa, the phenogram presented in Figure 14 gives a surprisingly accurate representation of the phylogenetic relationships of the species of Austromontana as envisioned in the present study. Of particular significance is the divergence of 4 distinct lines from A. cordifolia: A. cernua, A. nevadensis, A. latifolia and A. discoidea. In addition, the derivation of A. venosa and A. spathulata from A. discoidea is accurately represented.

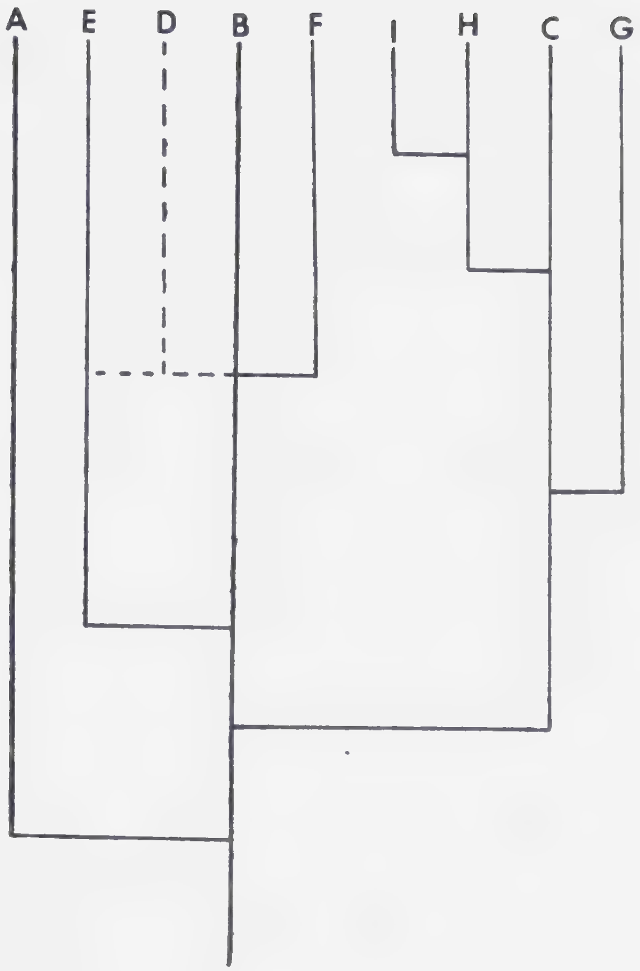


Figure 14. Phenetic relationships of the species of Arnica subgenus Austromontana using states of 0-2 for morphological and ecological characters and 0-1 for chemical characters. A- A. cernua, B- A. cordifolia, C- A. discoidea, D- A. gracilis, E- A. latifolia, F- A. nevadensis, G- A. spathulata, H- A. venosa, I- A. viscosa.

The position of A. viscosa relative to A. venosa in Figure 14 illustrates one of the major draw backs of strictly phenetic analyses. As Davis and Heywood (1963) note, they often fail to accurately represent convergences and parallelisms. Although not related, A. viscosa and A. venosa share several derived features including discoid heads, sessile leaves, woody caudex, a lack of innovations and adaptation to very dry habitats. These similarities reflect general evolutionary trends within both the genus Arnica and subgenus Austromontana but do not necessarily reflect phylogenetic relationships. Substrate specificity is another example of convergent evolution in Austromontana. Both A. cernua and A. spathulata are restricted to serpentne soils while A. viscosa occurs on volcanic pumice slopes. Substrate specificity is clearly a derived feature in Austromontana, however, results of the present study indicate that none of these three species are closely related.

In the groundplan-divergence method of Wagner (1961), the amount of advancement is expressed on a cladogram by divergence levels of the species, with the lengths of the branches equalling the total divergences. The divergence level is the sum of all clear-cut changes, including parallelisms, reversals and convergences, as well as non-parallel or uniquely derived character states (Wagner, 1980). Recently, Wagner (1980) has provided a review of the methodology and philosophy of the ground-plan divergence method as well as a new technique for the treatment of hybrids. The method may be summarized as follows:

A. Systematic analysis, based on taxonomy.

  Step 1. Phenetic classification.

  Step 2. Detection and removal of hybrids.

B. Determination of the common ancestor.

  Step 3. Analysis of individual character trends.

  Step 4. Combination of groundplan character states.

C. Phylogenetic synthesis based upon divergences.

  Step 5. Calculation of divergence levels.

  Step 6. Grouping by shared divergences.

  Step 7. Insertion of hybrid connections.

Correct phenetic classification using time honored taxonomic procedures underlies any phylogenetic analysis (Whiffen and Bierner, 1972; Gardner and LaDuke, 1978; Wagner, 1980). As Wagner (1980) notes, "a cladogram is no better than the quality of the taxonomy upon which it is based." Proper delimitation of species as well as the detection of hybrids can only be made with a thorough understading of the taxa under study. Wagner (1980) notes that hybrids, due to their intermediate characters, tend to break down the complexes of divergences that have arisen in separate lines of evolution. He therefore advocates removing hybrids from cladistic analysis until the cladogram of divergent species is constructed, so as not to obscure the phylogenetic picture. In the present investigation, _A. gracilis_ is treated as a probable hybrid between _A. cordifolia_ and _A. latifolia_. However, for reasons to be

subsequently discussed, this species is treated in the same manner as the other eight species.

In the present study a total of 27 morphological, ecological and chemical characters have been used in cladistic analysis (Table 12). States considered pleisomorphous have been designated 0, apomorphous states have been given a value of 1 and intermediate states have been assigned a value of 0.5 (Table 17). Morphological and ecological character trends have previously been discussed. Harborne (1977) notes a general trend in flavonoid advancement from flavonols → flavones → increased methylation and 6-hydroxylation. However, at present it is not possible to place an absolute ranking of advancement on a given series of flavonoids, particularly flavones. For example, it is not possible to determine which is the most advanced out of a 3' or 4' or 6' or 7' methyl Luteolin. Therefore, for purposes of cladistic analysis, the flavonoid data for the subgenus Austromontana has been reduced to six categories of advancement based on increasing methylation and 6 hydroxylation. Wagner (1980) notes that cladistic analysis should take into account reductions. Therefore an additional character to account for secondary reductions in flavonoid profiles has been added. For example, A. cernua has what appears to be the most plesiomorphous flavonoid profile in Austromontana, however this is probably the result of genetic depletion in this rare species.

The determination of the common ancestor is made by combining all the groundplan (plesiomorphous) characters (Wagner, 1980).

Table 12. Characters and states used in cladistic analysis of *Arnica* subgenus *Austromontana*

Character	(Plesiomorphous) State 0	(Apomorphous) State 1
A Head: shape	campanulate	turbinate
B number	1-3	> 7
C type	radiate	discoid
D Pappus: color	white	white-tawny
E setae	barbellate	barb.-subplumose
F Stem branching	-	+
G Leaf position	below midstem	evenly distributed
H Underground parts	rhizome	caudex
I Innovations	+	-
J Leaves: # pairs	2-4	> 6
K margin	dentate	entire
L shape	cordate	broadly lanceolate
M petioles	narrow	sessile
N Disc florets: #	> 50	< 25
O color	yellow	cream
P Phyllaries: shape	ovate-lanceolate	lanceolate
Q vestiture	gland.+non-gland.	glandular
R Achene: color	dark grey	brown or black
S glandular hairs	-	+

T Ecology	mesic	dry
U Substrate specificity	-	+
V Flavone glycosides	-	+
W Flavone mono-Me	-	+
X Flavone di-Me	-	+
Y Flavone tri-Me	-	+
Z 6-hydroxylation	-	+
Z' Flavonoid reduction	-	+

Table 17 . Character states, divergence formulae and divergence levels used in cladistic analysis of the nine species of *Arnica* subgenus *Austromontana*

	CHARACTER STATES																											
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z	Z'	Divergence formula	Divergence level
A. cernua	0.5				1						0.5			0.5						0.5	1						1	A/2 E K/2 N/2 T/2 U Z'	5
A. cordifolia																			0.5			1	1					S/2 V W	2.5
A. discoidea	0.5	0.5	1		1	0.5				0.5	0.5	1		0.5					1	0.5		1	1	1				A/2 B/2 C F/2 J/2 K/2 L N/2 S T/2 V W X	10 5
A. gracilis	0.5	1				1					0.5	1		1			1	1	1	1		1	1	1				A/2 B F K/2 L N Q R S T V W X	12
A. latifolia	1	0.5									0.5		1			1		1	0.5				1					A B/2 K/2 M P R S/2 W	6.5
A. nevadensis	0.5			1	1						1			0.5		0.5	1		1	0.5			1					A/2 D E K N/2 P/2 Q S T/2 W	8
A. spathulata	0.5	0.5	1			0.5				0.5		0.5	0.5	0.5		0.5	0 5	1	1	0.5	1		1	1			1	A/2 B/2 C F/2 J/2 L/2 M/2 N/2 P/2 Q/2 R S T/2 U W X	12
A. venosa	0.5	0.5	1			0.5	1	1	1	1	0.5	0.5	1	0.5						1		2	1				1	A/2 B/2 C F/2 G H I J K/2 L/2 M N/2 T W Z'V	14
A. viscosa	1	1	1	1	1	1	1	1	1	1	1	0.5	1	1	1	1	1			1	1		1	1	1	1		A B C D E F G H I J K L/2 M N O P Q T U W X Y Z	22 5

This hypothetical ancestor, which theoretically would have values of 0 for all 27 characters of the subgenus, serves as the base point of the cladogram. The divergence level for each species is calculated by summing its derived character states (Table 17). The species are then placed on the cladogram based on their divergence level. The branching points are determined by the shared derived character states. The final step in the construction of the cladogram is the placing of the hybrid taxa. According to Wagner (1980) hybrids usually have all of the elements of the divergence formulae of the parents and therefore their divergence level should be the same as, or exactly intermediate between the parents. However, this is probably only true for very recent first generation hybrids that have not undergone subsequent introgression. This hypothesis also assumes that hybrids do not proceed to evolve on their own because they are usually sterile (Wagner, 1980). As previously suggested, _A_. _gracilis_ is probably the result of introgression or backcrossing with _A_. _latifolia_ and now, due to apomixis, behaves as a distinct, self-perpetuating species that has become fairly widespread in the central Rocky Mountains. Therefore, it is not surprising that _A_. _gracilis_ shares few features with its parents and has a much higher divergence level. It has therefore been treated the same as a divergent species and placed on the cladogram according to its divergence level.

The completed Wagner dendrogram for the nine species of _Arnica_ subgenus _Austromontana_ is presented in Figure 15. It is felt that Figure 15 gives a fairly accurate representation of the various

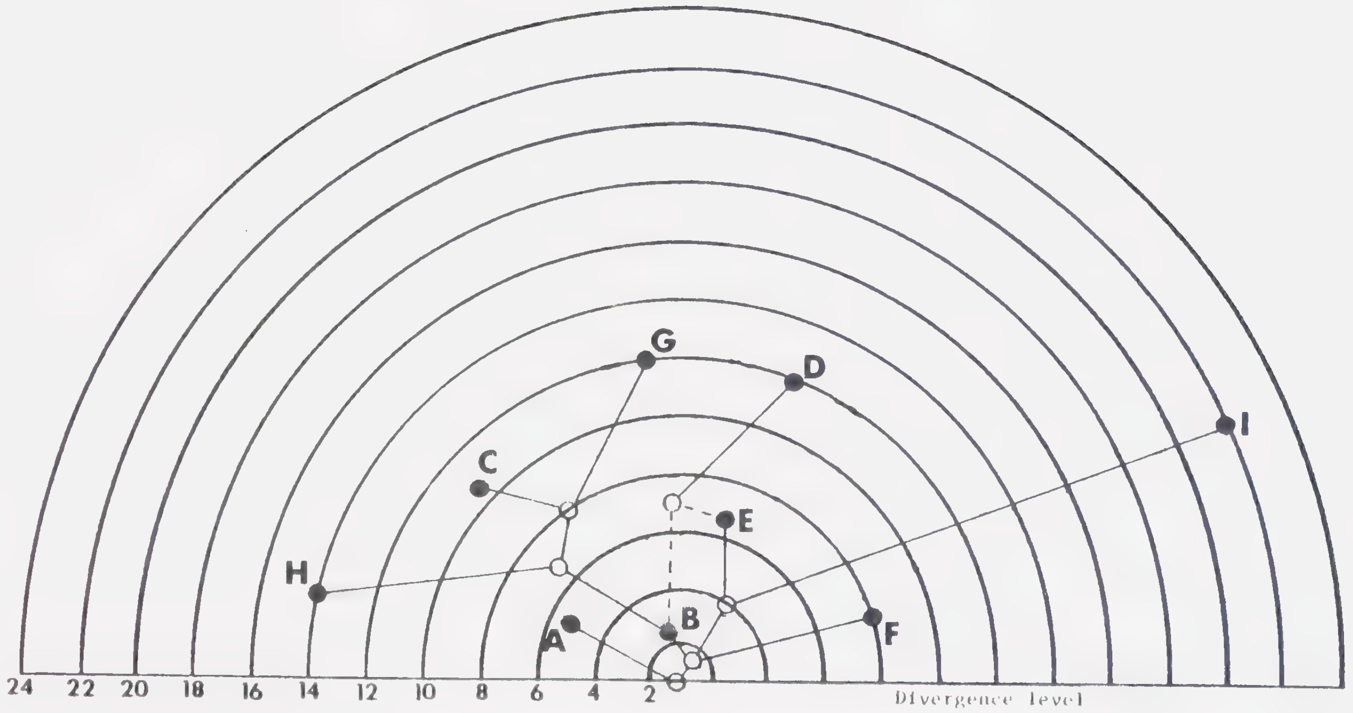


Figure 15. Proposed phylogenetic relationships of the species of *Arnica* subgenus *Austromontana*.

A- *A*. *cernua*, B- *A*. *cordifolia*, C- *A*. *discoidea*, D- *A*. *gracilis*, E- *A*. *latifolia*, F- *A*. *nevadensis*, G- *A*. *spathulata*, H- *A*. *venosa*, I- *A*. *viscosa*.

relationships and levels of evolutionary advancement of the species of *Austromontana*. As previously noted, *A. cordifolia* probably represents the "archetypal" *Austromontana*. This is reflected in its very low divergence level which places it very close to the hypothetical ancestor of the subgenus. *Arnica cernua* is only slightly more advanced than *A. cordifolia*. This is due largely to its longer pappus seta and derived ecology. *Arnica latifolia* with its narrow heads, sessile leaves and brown achenes is only slightly more advanced than *A. cordifolia*. Although often mistaken for *A. cordifolia*, *A. nevadensis* is readily distinguished by its tawny, sub-plumose pappus and entire leaves, all of which represent derived features. Interestingly, the discoid condition has been accompanied by several other derived features including highly methylated flavones; narrower, broadly petiolate or sessile leaves and an ecological shift to drier habitats. Consequently, all the discoid species have relatively high divergence levels. *Arnica discoidea*, which sometimes resembles a rayless *A. cordifolia*, has a divergence level only slightly less than its two derivatives *A. venosa* and *A. spathulata*. As previously noted, *A. viscosa* possesses virtually every derived feature of the subgenus *Austromontana*. This is readily apparent from its very high divergence level and position on the cladogram. *Arnica viscosa*'s immediate ancestor is not readily discernable, however, since it shares several features with *A. latifolia* including sessile leaves, narrow heads, relatively high altitude habitat and Quercetin 6-methyl ether 3-0-gluco-

side, it is most likely derived from the latter. There is little doubt that *A. gracilis* is the product of hybridization between *A. cordifolia* and *A. latifolia*. However, since the former has apparently undergone further evolution subsequent to its formation, it has a relatively high divergence level.

TAXONOMY

ARNICA Linnaeus, Sp. Pl. 884. 1753

Perennial herbs; stems simple to many branched; fibrous-rooted. Leaves simple, opposite (sometimes basal) or the uppermost reduced and sometimes alternate, sessile and narrowly petiolate. Heads solitary or numerous in a corymbiform inflorescence, radiate or discoid, hemispheric to turbinate; involucral bracts herbaceous, more or less biseriate; receptacle convex, naked; ray florets pistillate, ligules yellow to orange; disc florets perfect, yellow to orange or rarely cream colored; anthers yellow or purple, entire or slightly sagittate at the base; style branches flattened, truncate or very shortly appendiculate, penicillate at the tip, papillose externally, and with ventro-marginal sigmatic lines; pappus of numerous white to tawny, barbellate to plumose capillary bristles. Achenes cylindric or nearly so, 5-10 nerved. Chromosome number *x* = 19. Type species: *Arnica montana* L.

Key to the subgenera of *Arnica*.

1. Anthers purple; involucral bracts callous tipped..... ... subgn. *Andropurpurea*.

1. Anthers yellow; involucral bracts acute to attenuate or obtuse . . . . 2.

2. Cauline leaves much reduced; leaves chiefly basal, rosulate, broadly elliptic to rhombic; species of central Europe and the Coastal Plain of eastern United States.....subgn. *Arnica*.

2. Cauline leaves well developed; leaves rather evenly distributed along stem, lanceolate to cordate; species of Boreal regions and western Cordillera of North America..............................3.

3. Pappus subplumose to plumose and tawny.....subgn. Chamissonis.

3. Pappus barbellate and white; rarely subplumose and tawny, if so then leaves broad and entire...................................4.

4. Leaves narrow, 3-10 times as long as wide........subgn. Arctica.

4. Leaves broad, 1-2.5 times as long as wide...subgn. Austromontana.

SUBGENUS Austromontana Maguire, Brittonia. 432. 1943. Type species: A. latifolia Bong.

Section Austromontana Maguire, Brittonia. 432. 1943.

Section Eulatifoliae Maguire, Brittonia. 432. 1943. Lectotype: A. latifolia Bong. (nom illegit).

Section Eradiatae Maguire, Brittonia. 452. 1943. Lectotypus novus: A. discoidea Benth.

Subgenus Calarnica Straley, 1980. Manuscript name.

Stems simple to much branched, arising from a scaly rhizome or woody caudex; cauline leaves relatively broad, 1.0-2.5 times as long as wide, cordate to narrowly ovate or spathulate, entire to dentate or crenate, sessile to broadly or narrowly petiolate, uppermost leaves often reduced and bract-like. Heads solitary or numerous in a corymbiform inflorescence, radiate or discoid, broadly campanulate to narrowly turbinate; involucral bracts ovate to lanceolate, acute to acuminate. Ray florets yellow; disc florets yellow or cream colored, anthers yellow; pappus white or rarely tawny, barbellate to subplumose. Achenes grey, brown or black, ± stipitate glandular and/or ± hirsute with duplex hairs.

Key to the species of subgenus Austromontana:

1. Heads discoid (marginal corollas sometimes ampliate).

2. Leaves sessile.

    3. Leaves toothed, veins conspicuous; achenes hirsute with duplex hairs; florets yellow...8. _A_. _venosa_.

    3. Leaves entire, veins inconspicuous; achenes stipitate glandular; florets cream colored..9. _A_. _viscosa_.

2. Leaves petiolate, the petiole sometimes broad.

    4. Lowermost leaves ovate to subcordate or broadly lanceolate; petioles narrow or scarcely winged; achenes dark grey, stipitate glandular with duplex hairs; species of southern Washington to southern California, including the Klamath region. 3. _A_. _discoidea_

    4. Lowermost leaves spathulate; petioles broad; achenes black, stipitate glandular, lacking duplex hairs; species mostly restricted to serpentine soils of the Klamath region........7. _A_. _spathulata_.

1. Heads radiate.

    5. Cauline leaves sessile, heads turbinate, achenes brown.... .....5. _A_. _latifolia_.

    5. Cauline leaves petiolate, heads campanulate to campanulate-turbinate, achenes dark grey or black.

        6. Leaves glabrous, thick, leathery; heads nodding in bud; plants restricted to serpentine soils of Klamath region.....1. _A_. _cernua_.

        6. Leaves variously pubescent, thin; heads erect in bud; plants not of serpentine soils, widespread.

            7. Stems several branched, mostly clumped; heads numerous (5-15); achenes black, mostly lacking duplex hairs.....4. _A_. _gracilis_.

            7. Stems mostly simple, not clumped; heads solitary or few (1-3); achenes dark grey with duplex hairs.

                8. Leaves cordate, toothed; heads broadly campanulate; involucral bracts ovate-lanceolate; pappus white, barbellate;

achenes ± hirsute and ± stipitate glandular; widespread cordilleran species............2. A. cordifolia.

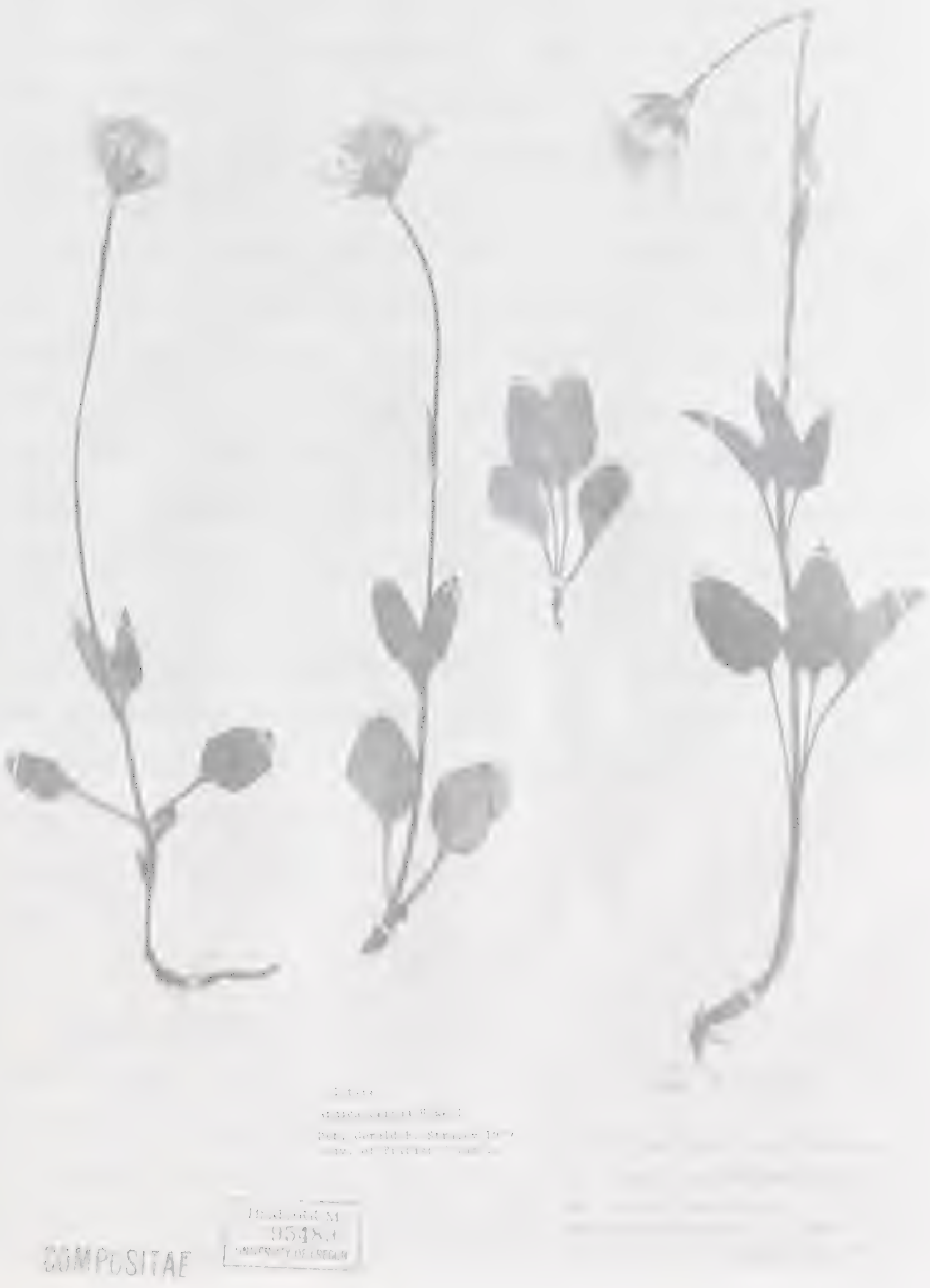
8. Leaves ovate to elliptic, entire; heads campanulate-turbinate; involucral bracts oblanceolate; pappus white to tawny, barbellate to subplumose; achenes stipitate glandular; species of Sierra Nevada, north less commonly to Washington ....6. A. nevadensis.

1. Arnica cernua Howell, Fl. NW. Am. 373. 1900 TYPE: Oregon, Josephine Co., On dry banks, base of the Coast mountains near Waldo, July 1884, T. Howell 166 (Holotype, ORE!) (Figure 16).

Arnica chandleri Rydb., N. Am. Fl. 34:339. 1927. TYPE: California, Humboldt Co., Hupi (Hoopa) Indian Reservation, June, 1901, H.P. Chandler 1298 (Holotype, NY!; Isotypes, UC!, US!).

Stems simple, rarely branched, often reddish-purple, 10-30 cm high, 1.5-2.5 mm diam., glabrous to sparsely villous; rhizomes 2-3 mm thick, 2-3 pairs reddish scales at the summit. Cauline leaves 3-4 pairs, often reddish-purple, elliptic to ovate, sometimes sub-cordate, 1.5-8 cm long, 1.5-4 cm broad, often thick and nearly succulent, glabrous to scabrous, acute to rounded, entire to serrate, commonly crenate or slightly lobed; petioles narrow or frequently broad winged on lowermost leaves, 2-6 cm long, 1-5 mm broad; uppermost leaves often reduced, lanceolate and sessile;

Figure 16. Holotype of _A_. _cernua_ Howell.

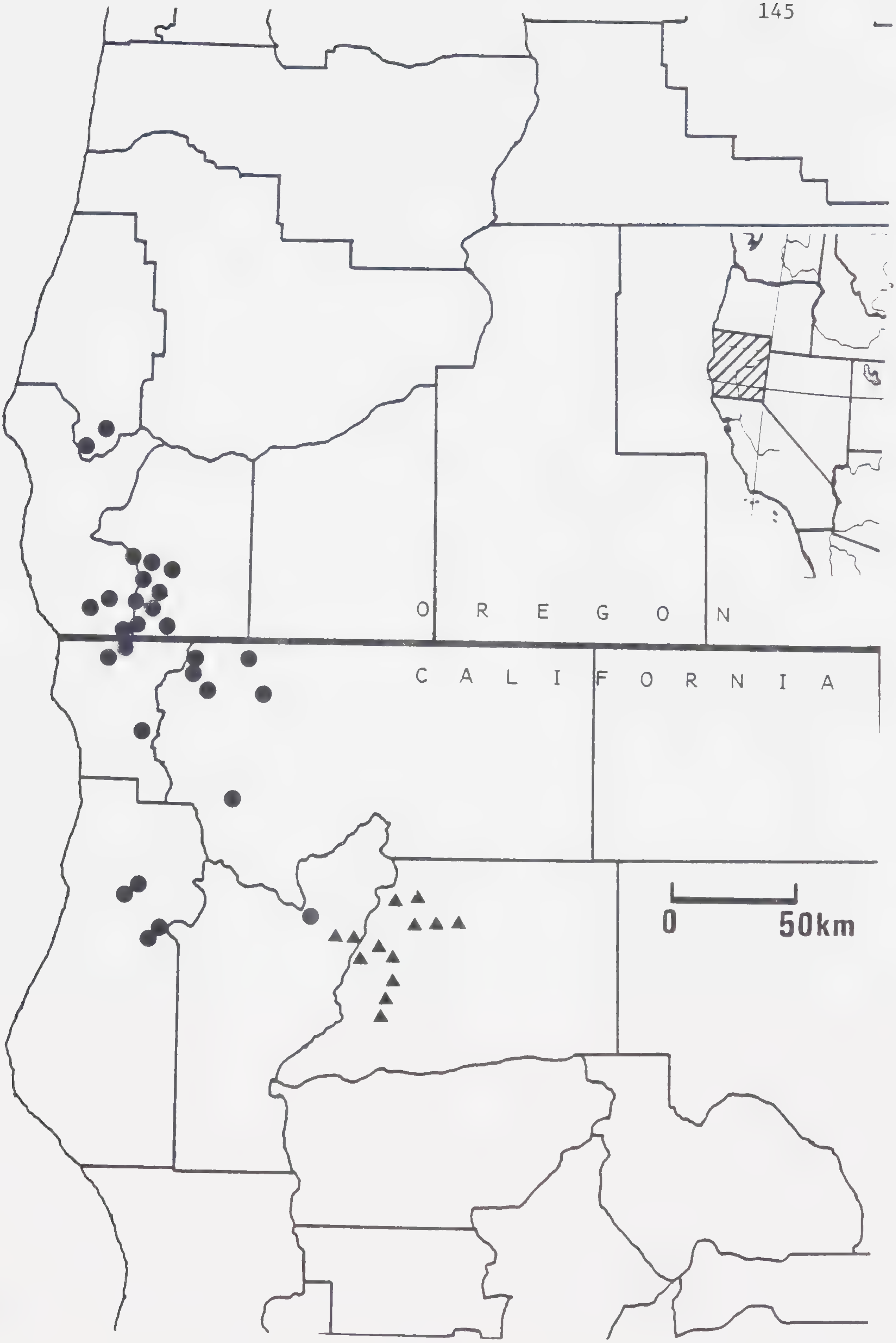

HERBARIUM
UNIVERSITY OF OREGON
COMPOSITAE

leaves of the innovations 4-8, similar to cauline leaves. Inflorescence usually a single head or corymb of 3-5 heads, often nodding; peduncle 3-15 cm long, sparsely to densely pilose and scabrous; heads radiate, campanulate-turbinate, 10-25 mm high; involucral bracts 8-14, ovate to broadly lanceolate, 8-16 mm long, 3-6 mm broad, sparsely to densely pilose and stipitate-glandular, acute to acuminate. Ray florets 5-10, yellow to slightly orange, broadly linear to elliptic, 10-20 mm long, 4-6 mm broad, 1-3 dentate; disc florets 20-60, yellow, tubular 10-15 mm long, villous below; pappus of both ray and disc florets white, barbellate to subplumose. Achenes dark grey, 6-8 mm long, 1 mm broad, sparsely to densely hirsute with duplex hairs. Chromosome number 2$\underline{n}$ = 38.

Ecology and Distribution: Relatively rare, but locally abundant in dry, open Pinus-Pseudotsuga menziesii forests at moderate elevations (500-1500 m). Known only from serpentine soils in Coos, Curry and Josephine counties, Oregon and Del Norte, Trinity and Siskiyou Counties, California (Figure 17). Flowers late April to June.

Arnica cernua is a relatively rare serpentine endemic of the Klamath region confined to relatively open, exposed habitats in Pinus-Pseudotsuga menziesii forests at elevations of 500-1500 m. It is easily distinguished by its glabrous, thick, ovate, crenate, petiolate leaves that are often reddish or purple; solitary, nod-

Figure 17. Distribution of A. cernua Howell (●) and A. venosa H. M. Hall (▲).


OREGON
CALIFORNIA
0
50km

ding heads; and serpentine habitat. Both Maguire (1943) and Straley (1980) insisted that *A. cernua* is derived from *A. latifolia*. However, both *A. cernua* and *A. cordifolia* share several features including: long petiolate leaves, broad solitary heads with pilose and stipitate glandular, ovate-lanceolate involucral bracts and dark grey achenes. In contrast, *A. latifolia* has sessile leaves, several narrow heads with narrow, sparsely pubescent bracts and brown achenes. In addition, the leaves of *A. cernua* are sometimes subcordate or even cordate (*T. Howell* *1446*, *1936* NDG) like *A. cordifolia*. It therefore seems more likely that *A. cernua* is more closely related to *A. cordifolia* rather than *A. latifolia*.

In the original description of *A. cernua* (Howell, 1900) no specimens were cited and no type was designated. Maguire (1943) designated a Howell collection (*T. Howell* *1446* UC, NDG) as the lectotype for this species. However, as Rollins (1972) noted, "the existence of a holotype in the institution where the author worked is assumed until proven otherwise." Examination of Howell's collections at the University of Oregon has revealed that he did in fact designate a type by writing "Typ[sic] specimen" on one specimen (*T. Howell* *166* ORE). According to the criteria of Rollins (1972) there would be no need to designate a lectotype since *Howell 166* would automatically be the holotype for *A. cernua*. The type sheet consists of three flowering stems and one basal rosette.

Rydberg (1927) described a smaller, more glandular form of *A. cernua* as *A. chandleri*. Examination of the type specimens

(Chandler 1298, NY, UC, US) as well as two other collections of this taxon (Davy and Blasdale 5645 UC and Tracy 7449 UC) indicates that they are all referable to A. cernua. Also, with respect to A. chandleri, no isotype of this taxon has been located by the staff at the Missouri Botanical Garden. This is in contradiction to previous reports by Straley (1980).

2. Arnica cordifolia Hook, Fl. Bor. Am. 1:331. 1834. TYPE: Alpine woods of the Rocky Mountains, on the east side, Drummond s.n. (Holotype, K photo!) (Figure 18).

Arnica macrophylla Nutt., Trans. Am. Phil. Soc. II. 7: 408. 1841. TYPE: Blue Mountains of Oregon, Nuttall s.n. (Holotype, K photo!).

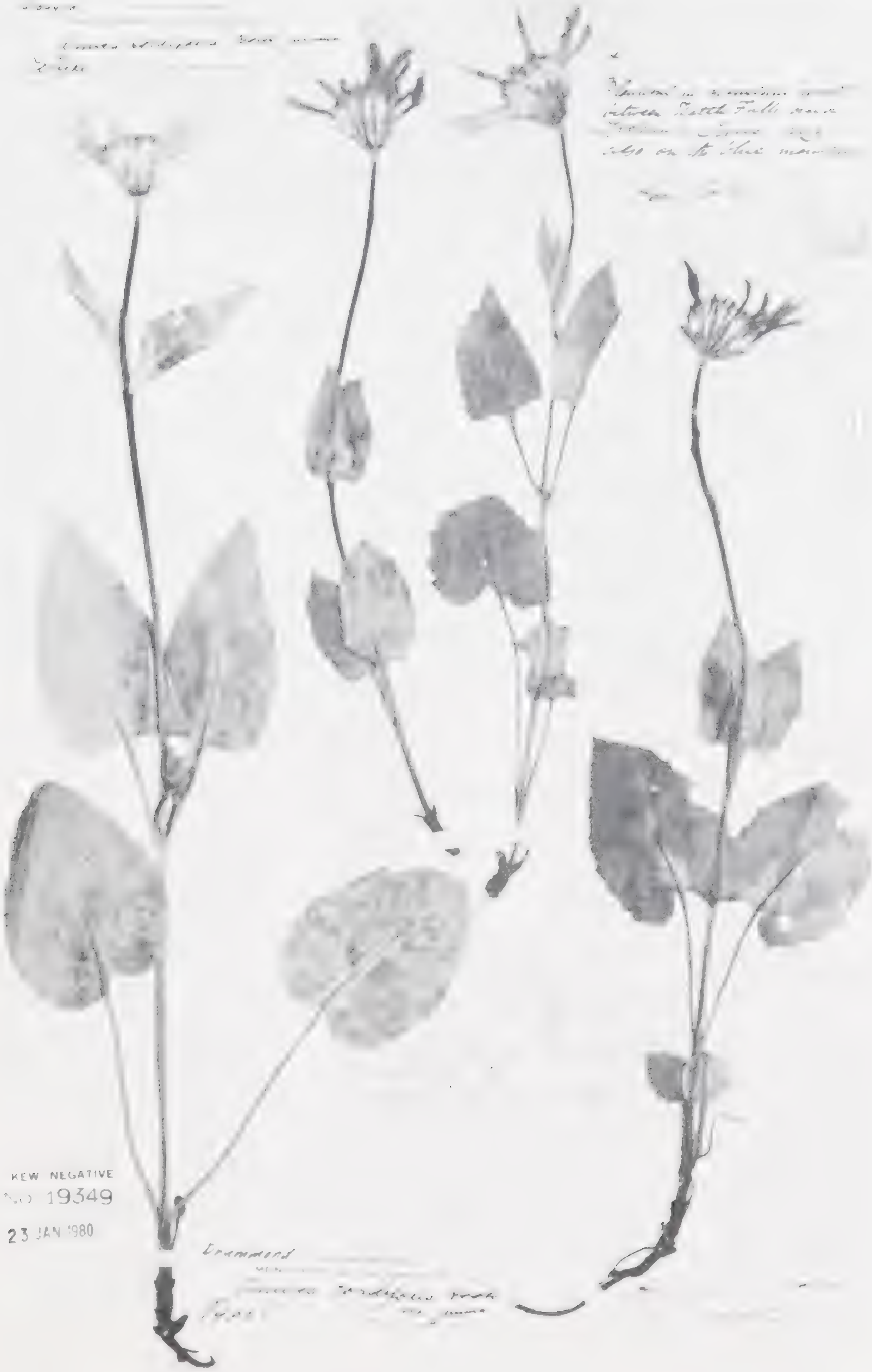
Arnica chionophila Greene, Pittonia 4:171. 1900. TYPE: Ruby Mountains, Nevada, July 20, 1896, E.L. Green s.n. (Holotype NDG!).

Arnica subcordata Greene, Pittonia 4:173. 1900. TYPE: on the Athabasca River, June 26, 1898, W. Spreadborough (Geol. Surv. Can. No. 19644) (Holotype, CAN!; Isotype, LCU!).

Arnica pumila Rydb., Mem. N.Y. Bot. Gard. 1:433. 1900. TYPE: Gray's Peak, Colorado, Aug.-Step., 1872, Torrey s.n. (Holotype, NY!).

Arnica parvifolia Greene, Pl. Baker. 3:28. 1901. TYPE: Marshall Pass, Colorado, 10,000 ft., July 19, 1901, C.F. Baker 515 (Holotype, NDG!; Isotypes CAS!, POM!, UC!, US!, WS!).

Figure 18. Holotype of A. cordifolia Hook.


between Tatth Falls
also on the mountains
Drummond
cordifolia
KEW NEGATIVE
NO 19349
23 JAN 1980

Arnica paniculata A. Nelson, Man. Bot. Rocky Mts. 572. 1909. TYPE: moist timber, Bridger Peak, Carbon Co., Wyoming, Aug. 24, 1903, L.N. Gooding 1974 (Holotype, RM!; Isotypes, CAS!, GH!, MO!, NY!, RM!, UC!, US!).

Arnica evermanii Green, Ottawa Nat. 23:215. 1910. TYPE: shores of Petit Lake, Idaho, Aug. 13, 1895, B.W. Evermann 318 (Holotype, US!).

Arnica abortiva Greene, Leaflets 2:47. 1910. TYPE: open spaces in timber, Wind River Mts., Wyoming, July 23, 1881 W.H. Forwood s.n. (Holotype: US!).

Arnica andersonii Piper, Proc. Biol. Soc. Wash. 33:106. TYPE: Skeena, British Columbia, Sept. 11, 1910, J.R. Anderson 677 (Holotype, US!; Isotypes US!, WS photo!).

Arnica austinae Rydb., N. Am. Fl. 34:340. 1927. TYPE: Lake City Canyon, California, July 1898, Austin and Bruce 2165 (Holotype, NY!; Isotypes NY!, UC!).

Arnica humilis Rydb., N. Am. Fl. 34:341. 1927. TYPE: on the saddle, Lake Louise, Alberta, July 20, 1904, J. Macoun (Geol. Surv. Can. No. 65504) (Holotype, NY!, Isotype CAN!).

Arnica whitneyi Fernald, Rhodora 37:334. 1935. TYPE: dry deciduous woods near Copper Harbor, Keweenaw Co., Michigan, July 4,1934 (Holotype, GH!).

Arnica hardinae St. John, Fl. SE. Wash. 419. 1937. TYPE: open woods, Lake Chatcolet, Benewah Co., Idaho, Oct. 2, 1927, G. Weitman 226 (Holotype, WS!).

Arnica cordifolia Hook. var. pumila (Rydb.) Maguire, Madroño 6: 154: 1942.

Arnica cordifolia Hook. var. whitneyi (Fernald) Maguire, Brittonia 4:452. 1943.

Arnica cordifolia Hook. var. macrophylla (Nutt.) Maguire, Am. Midl. Nat. 37:137. 1947.

Arnica cordifolia Hook. var. humilis (Rydb.) Maguire, Am. Midl. Nat. 37:138. 1947.

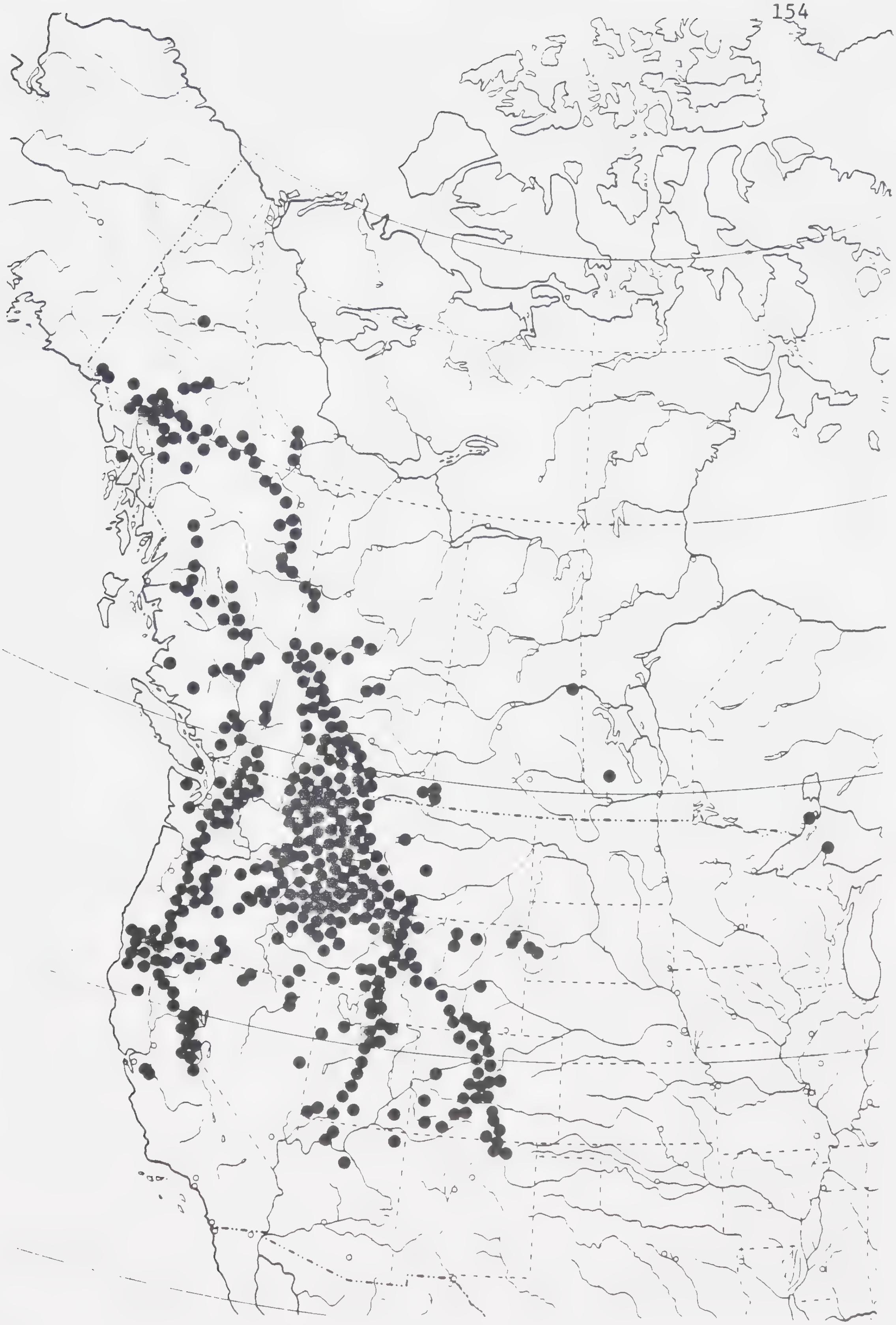
Stems mostly simple, sometimes branched, 10-40 (70) cm high, 2-3 mm diam., glandular-puberulent to densely villous especially above; rhizomes long, giving rise to several basal rosettes and flowering stems, 1.5-3.0 mm thick, 2-3 pairs of thin brown scales and often old leaf bases at the summit. Cauline leaves 2-4 (6) pairs, cordate or subcordate to narrowly ovate, 3-10 cm long, 2-10 cm broad, puberulent to sparsely villous and sometimes stipitate-glandular especially above, acute to rounded, entire to usually dentate, sometimes coarsely dentate; petioles (2) 5-10 (20) cm long; uppermost leaves often reduced, ovate-lanceolate, short-petiolate or sessile, sometimes bract-like; leaves of the innovations 2-4, similar to cauline leaves or often more coarsely dentate. Inflorescence usually a single head or corymb of 3-5 (10) heads; peduncle 4-20 cm long, pilose and stipitate glandular; heads radiate, broadly campanulate, 1.5-3.0 cm high; involucral bracts, 10-20, narrowly ovate to lanceolate, 10-20 mm long, 2-5 mm broad,

pilose at base to puberulent above, sometimes glandular, acute to acuminate, margins scarious. Ray florets 6-13, yellow, elliptic-oblong, 15-30 mm long, 5-10 mm broad, subentire to 3-dentate; disc florets numerous, 20-90, yellow, tubular, 9-12 mm long, sparsely glandular above, sparsely to densely villous and stipitate glandular below; pappus of both ray and disc florets white, barbellate. Achenes dark grey, 5-10 mm long, 1 mm broad, sparsely to densely hirsute with duplex hairs, also sometimes stipitate glandular. Chromosome number $2\underline{n}$ = 38, 57, 76, 95, 114.

Ecology and Distribution: Very common in mesic *Picea* - *Pinus* -*Pseudotsuga* *menziessi* forests or occasionally sub-alpine meadows from the central Yukon south through northern New Mexico, northern Arizona, Nevada and northern California. Also found in the Cypress Hills of Alberta and Saskatchewan and with outlying populations in the Black Hills of South Dakota, the Pasquia Hills of Saskatchewan and Riding Mt. Provincial Park, Manitoba. Also found in *Abies* *balsamea* - *Betula* - *Acer* forests in Keweenaw County, Michigan and Sibley Provincial Park, Ontario (Figure 19). Elevational distribution from 500 m in the Yukon to 3000 m in Colorado. Flowers May-July.

Arnica *cordifolia* is probably the most widespread *Arnica* in western North America, occupying fairly mesic habitats in *Pinus* - *Pseudotsuga* *menziesii* or *Picea* forests throughout most montane

Figure 19. Distribution of _A_. _cordifolia_ Hook.



areas of the region. In such areas as the foothills of Alberta, it forms extensive, nearly continuous populations for many kilometers. In the east *A. cordifolia* is restricted to only a few populations in *Betula* - *Acer* forests of Keweenaw Co., Michigan and Sibley Provincial Park, Ontario. *Arnica cordifolia* has also been recently collected in the Pasquia Hills, east of Saskatoon, Saskatchewan (*J. Rowe 983* CAN) and in Riding Mountain Provincial Park, Manitoba (*A. Lovaas 61-8* DAO).

In its typical woodland habitat, *A. cordifolia* displays little variability and is easily recognized by its large, solitary heads with broad rays and its cordate, dentate leaves. However, as previously noted, when it occurs in more exposed or distributed habitats the leaves become smaller, narrower and lose their cordate bases; the pubescence becomes denser, harsher and more glandular; and the plants become smaller and more branched with several heads. Most of the triploids reported in Table 5 are of this type. Higher elevation forms of *A. cordifolia* tend to be much reduced, lack cordate leaf bases and have entire leaves. This form has previously been recognized as *A. pumila* Rydb. or as *A. cordifolia* Hook. var. *pumila* (Rydb.) Maguire. However, when such plants are transplanted to the greenhouse they revert to typical *A. cordifolia* (cf. *S. Wolf 306* ALTA). The high altitude form has often been confused with *A. nevadensis*, particularly in the mountains of Utah. However, the latter can be recognized by its narrower heads, oblanceolate phyllaries, less pubescent leaves and darker pappus with longer setae.

According to Maguire (1943), Drummond's explorations were largely in the vicinity of Jasper House, Alberta, along the Upper Athabasca River and at the headwaters of the North Saskatchewan River. Bird (1967) also concluded that most of Drummond's collections from the "Rocky Mountains" probably came from Jasper National Park. The type of *A. cordifolia* from "Alpine woods of the Rocky Mts.", was therefore probably collected in the front range of the Rocky Mountains, probably in Jasper National Park, Alberta. The type sheet consists of four specimens, the holotype collected by Drummond and three specimens collected by Douglas on the same expedition. The holotype represents a typical woodland form of *A. cordifolia* with a single head and three pairs of leaves, the lower cordate and the upper reduced. The other specimens are all also typical *A. cordifolia*.

Arnica macrophylla Nutt. is merely a large leaved, typical *A. cordifolia*.

Neither Maguire (1943) nor Straley (1980) had examined the type of *A. chionophila* Greene. However, based on Greene's (1900) description and the fact that the type was collected at high altitude, both included this epithet in the synonymy of *A. nevadensis*. Examination of the holotype of this taxon from Greene's herbarium (NDG) has revealed that it is a dwarf, high altitude form of *A. cordifolia*.

Straley (1980) considered *A. grandifolia* to be a probable hybrid between *A. cordifolia* and *A. latifolia*. However, the holo-

type of *A. grandifolia* (NDG) as well as the isotypes at the U.S. National Herbarium and Missouri Botanic Garden are *A. latifolia* while the isotype at the N.Y. Botanic Garden is *A. cordifolia*. This taxon has therefore been included in the synonymy of *A. latifolia*.

Arnica subcordata Greene is merely a small form of *A. cordifolia* and can be recognized by its large, solitary head and sub-cordate, petiolate leaves.

In his original description of *A. pumila*, Rydberg (1900) noted that this taxon was very closely related to *A. cordifolia* but differed in its small size and sub-entire, narrow, non-cordate leaves. Maguire (1942) treated reduced, high altitude forms of *A. cordifolia* as variety *pumila*. However, as previously noted this habit is typical of high altitude populations of *A. cordifolia* and does not warrant taxonomic recognition.

Arnica parvifolia Greene also represents a high altitude form of *A. cordifolia*. The type sheet (NDG) contains three specimens that demonstrate the transition from typical cordate, dentate leaves to the small ovate, entire leaves characteristic of high altitude populations of *A. cordifolia*.

Maguire (1943) considered the rare *A. paniculata* A. Nelson a distinct species, while noting it may be a hybrid between *A. cordifolia* and *A. parryi* A. Gray. Ediger and Barkley (1978) considered this taxon a hybrid and therefore did not give it taxonomic recognition. Straley (1980) suggested that *A. paniculata* could

fall within the range of variation of A. cordifolia and therefore reduced it to synonomy under the latter. In fact, with the exception of its numerous heads and ovate leaves, A. paniculata differs very little from A. cordifolia as circumscribed in the present study. Additionally, a chromosome voucher of an A. cordifolia population with 2n = ca. 97 (T. Mosquin and J. Gillett 5425, La Plata Co., Colorado; UBC) bears considerable resemblance to the type collection of A. paniculata (L.N. Gooding 1974, Carbon Co., Wyoming). It is very likely that A. paniculata represents an A. cordifolia with a high chromosome number and/or the product of introgression between the latter and some other taxon. Arnica paniculata is therefore reduced to synonymy under A. cordifolia.

Maguire (1943) tentatively treated A.O. Garrett 1981, Salt Lake Co., Utah (NY) as A. paniculata. This specimen represents a broad leaved A. fulgens Pursh.

Arnica evermanii Greene represents the high altitude form of A. cordifolia with entire, ovate leaves.

Arnica abortiva Greene, A. andersonii Piper and A. austinae Rydb. all represent fairly typical forms of A. cordifolia while A. humilis Rydb. from Lake Louise, Alberta represents the high altitude form.

Arnica whitneyi of Keweenaw Co., Michigan was first described by Fernald (1935). It occurs as one large discontinuous population between Copper and Eagle Harbors (Straley, 1980). Recently it has also been located in Sibley Provincial Park, Ontario (Garton 15164

CAN, 15486 MICH). Maguire (1943) noted that this taxon differed little from western populations of *A. cordifolia* but retained it as a subspecies of the latter because of its disjunct distribution. Both Ediger and Barkley (1978) and Straley (1980) did not give this taxon formal taxonomic recognition. The fact that these eastern populations represent very typical *A. cordifolia*, share similar chromosome numbers and flavonoid chemistry with *A. cordifolia* and intervening populations of *A. cordifolia* in Saskatchewan and Manitoba also exist, supports Ediger and Barkley's (1978) treatment. In the present study *A. whitneyi* is therefore reduced to synonymy under *A. cordifolia*.

The type specimen of the last proposed *Arnica* species, *A. hardinae* St. John, is a typical woodland form of *A. cordifolia*. This name is therefore reduced to synonymy under the latter.

Two taxa placed in synonymy with *A. cordifolia* by Straley (1980) are considered synonyms of *A. mollis* Hook.

Arnica granulifera Rydb., Fl. Rocky Mts. 978. 1917. TYPE: Long Baldy, Little Belt Mountains, 7-8,000 ft., Aug. 19, 1896, *J.H. Flodman s.n.* (Holotype, NY!) is *A. mollis* Hook. and can be recognized by its broad heads, irregularly dentate leaves and tawny, subplumose pappus. Additionally, the type of *A. ovalis* Rydb., N. Am. Fl. 34:338. 1927. TYPE: Crows Nest Pass, Canadian Rocky Mts., *Macoun* (*Can. Geol. Surv. No. 72719*) (Holotype: CAN photo!), unseen by Straley, is also *A. mollis*.

3. *Arnica discoidea* Benth., Pl. Hartw. 319. 1849. TYPE: Monterey, California, *Hartweg 1805* (Holotype, K photo!; Isotypes, GH photo!, NY!) (Figure 20).

Arnica parviflora A. Gray, Proc. Am. Acad. 7:363. 1867. TYPE: Chaparral, Humboldt Co., California, Geol. Surv. Calif. 1867. *H.N. Bolander 6051* (Holotype, GH!; Isotypes, UC!, K photo!, US!).

Arnica cordifolia Hook. var. *eradiata* A. Gray, Syn. Fl. N. Am. 1: 381. 1884. TYPE: Hood River, Oregon, 1884, *Mrs. Barrett s.n.* (Holotype, GH!).

Arnica grayi A. Heller, Muhlenbergia 1:5. 1900. TYPE: Hood River, Oregon, 1884, *Mrs. Barrett s.n.* (Holotype, GH!).

Arnica falconaria Greene, Ottawa Nat. 23:215. 1910. TYPE: Falcon Valley, Washington, June 27, 1892, *W.N. Suksdorf 1617* (Holotype, US!; Isotypes, UC!, GH photo!, NY!).

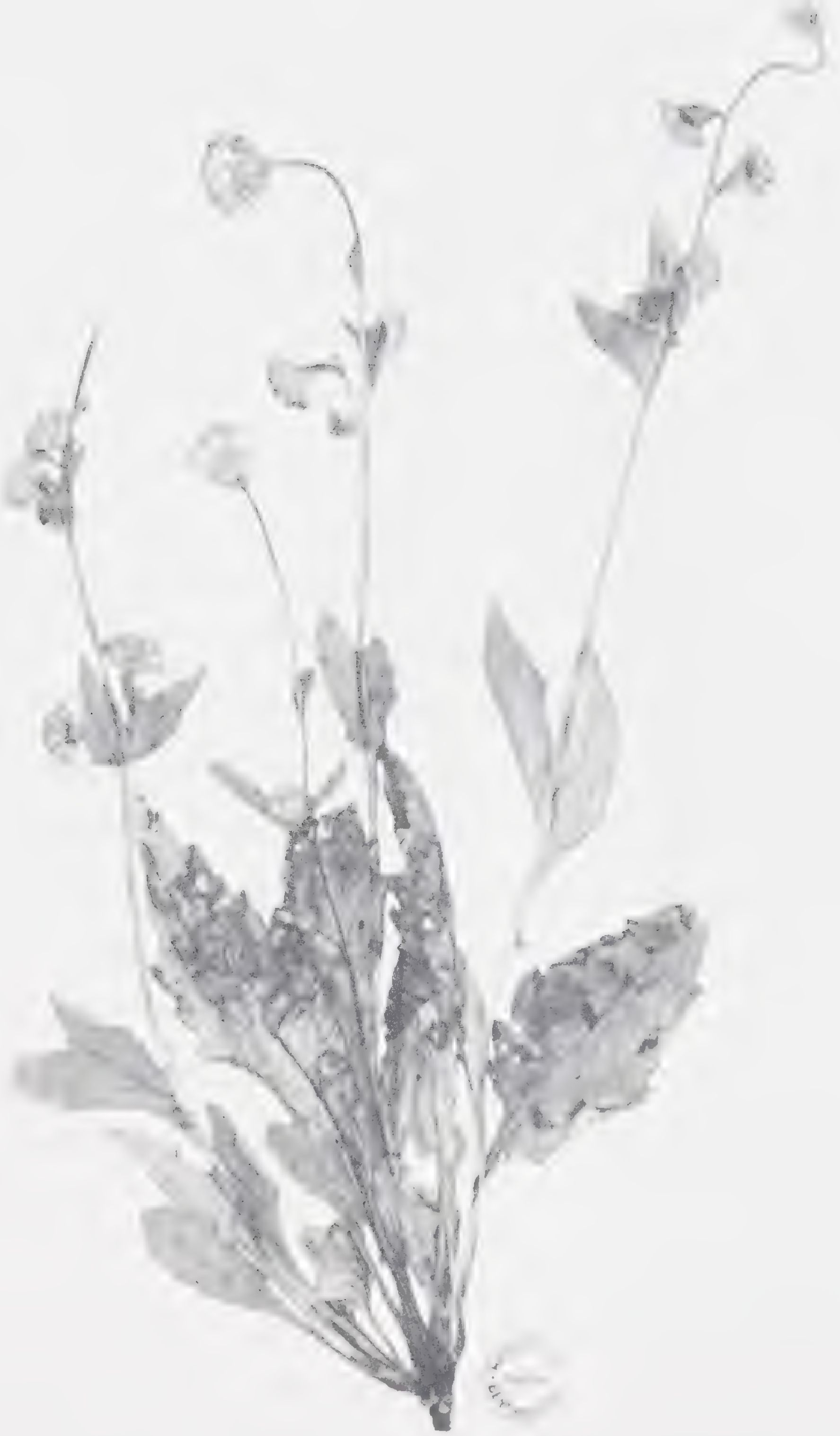
Arnica sanhedrensis Rydb., N. Am. Fl. 34:342. 1927. TYPE: foothills of Mt. Sanhedren, Lake Co., California, *Heller 5985* (Holotype, NY!; Isotypes, POM!, UC!, US!).

Arnica parviflora A. Gray subsp. *alata* (Rydb.) Maguire, Brittonia 4:455. 1943.

Arnica discoidea Benth. var. *eradiata* (A. Gray) Cronquist, Vasc. Pl. Pac. NW. 5:49. 1955.

Arnica discoidea Benth. var *alata* (Rydb.) Cronquist, Contr. Dudley Herb. 5:102. 1958.

Figure 20. Holotype of _A_. _discoidea_ Benth.



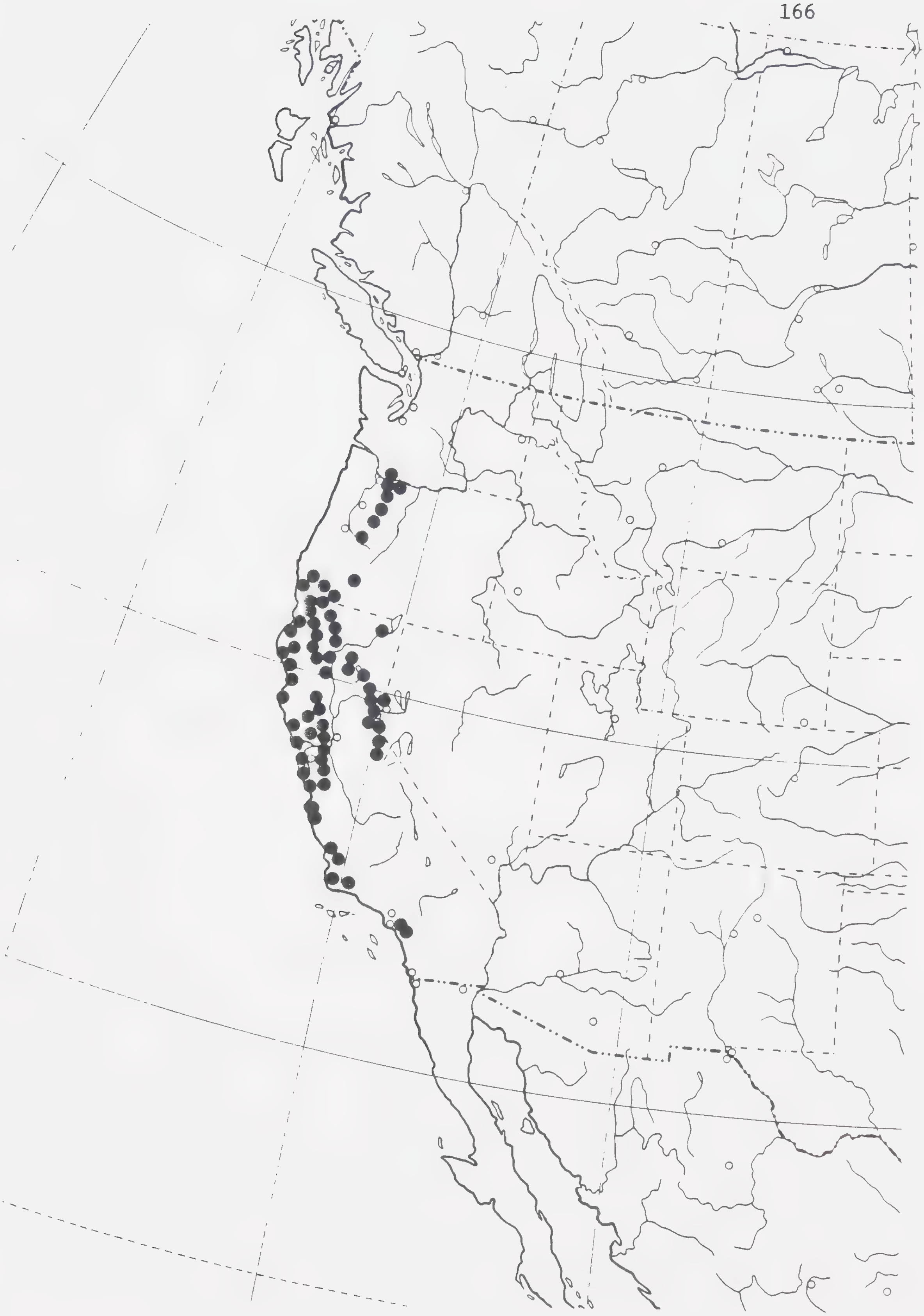
Stems mostly simple to branched above, 15-60 cm tall, 2-5 cm diam., villous and stipitate glandular throughout; rhizomes giving rise to numerous basal rosettes and flowering stems, 2-5 mm thick, scales and old leaf bases crowded toward the summit. Cauline leaves 3-7 pairs, sometimes crowded toward stem base and often reduced above, ovate to broadly lanceolate, seldom subcordate, 2-12 cm long, 1-7 cm broad, glabrate to pilose and stipitate glandular. serrate to coarsely dentate or crenate, rarely subentire; petioles narrow, 1.5-8.0 cm long, often broadly winged on upper leaves; leaves of the innovations 4-10; similar to cauline leaves. Inflorescence a corymb of 3-10 (30) heads; peduncle 2-15 cm long, stipitate glandular and densely pilose; heads discoid, the marginal corollas sometimes ampliate, turbinate-campanulate, 12-22 mm high; involucral bracts 8-15, ovate-lanceolate to narrowly lanceolate, 8-13 mm long, 1-4 mm broad, densely pilose and stipitate glandular, acute to acuminate. Florets 20-50, yellow, tubular, 8-11 mm long, stipitate glandular and sparsely to densely villous; pappus white, barbellate to subplumose. Achenes dark gray, 6-8 mm long, 1 mm broad, stipitate glandular and hirsute with duplex hairs. Chromosome number $2\underline{n} = 38, 57, 76$.

Ecology and Distribution: Relatively uncommon in moderately dry Quercus - Pinus forests or relatively exposed Chaparral from Klickitat County in southern Washington, south sparingly in the Cascades to northern California. Slightly more common in the Coast

Ranges of California south to Orange County (Figure 21). Elevational distribution ranges from near sea level to 1500 m. Flowers May-July.

Arnica discoidea is an extremely variable species and occurs in a variety of habitats from open chaparral to conifer forests from near sea level to 1500 m. As early as 1884 Gray recognized the similarity of this taxon to *A. cordifolia* and noted that "northwardly it seems to pass into *A. cordifolia*." Indeed, in southerly portions of its range, *A. discoidea* is quite distinct and can easily be recognized by its narrowly ovate leaves that are mostly crowded toward the base of the stem; broadly winged and reduced upper leaves; often numerous, narrower heads and frequently branched upper stem. However, northward it sometimes resembles little more than a rayless *A. cordifolia*. Further complicating its identification is the fact that ampliate marginal disc florets occur infrequently on some specimens of *A. discoidea* (e.g., *J.H. Thomas 4130* CAS and *H.M. Hall 9485* UC). When pressed, these florets resemble rays, causing some specimens to be erroneously identified as *A. cordifolia*. However, as previously noted, *A. discoidea* and *A. cordifolia* are distinct with respect to ecology, geographical distribution, flowering periods and a combination of several morphological features. *Arnica discoidea* occurs in hotter, drier, more exposed habitats at lower elevations west of the Sierras and Cascades and flowers 1-2 months later than *A. cordifolia*.

Figure 21. Distribution of A. discoidea Benth.



Based largely on leaf shape and geographical distribution, Maguire (1943) recognized four taxa within *A. discoidea sensu lato*: *A. grayi*, *A. discoidea sensu stricto*, *A. parviflora* ssp. *parviflora* and *A. parviflora* ssp. *alata*. Ediger and Barkley (1978) recognized the latter three taxa as varieties of *A. discoidea*: var *discoidea*, var. *eradiata* (which included *A. grayi*) and var. *alata* respectively. In the present study, an attempt was made to delimit the four taxa recognized by Maguire (1943). However, no correlations between morphology, chromosome number, geography or flavonoid chemistry were noted. This supports the treatment of *A. discoidea* as one highly polymorphic species.

The type sheet of *A. discoidea* (K) consists of one specimen with narrowly ovate leaves crowded toward the base; reduced, broadly winged upper leaves; and several relatively narrow heads typical of this species. Likewise, the isotype at the New York Botanical Garden represents a typical *A. discoidea*. Maguire (1943) noted the presence of an additional isotype at the Gray Herbarium however, it has not subsequently been located.

The type sheet of *A. parviflora* consists of two specimens, both with narrow leaves crowded at the base and several narrow discoid heads typical of *A. discoidea*.

The type sheet of *A. cordifolia* var. *eradiata*, which also serves as the type for *A. grayi*, consists of one specimen with ovate lower leaves, reduced broadly-winged upper leaves as well as several narrow discoid heads typical of *A. discoidea*.

The types of *A. falconaria*, *A. alata* and *A. sanhedrensis*, with relatively broad, cordate to sub-cordate leaves superficially resemble *A. cordifolia*; however, all have broadly winged, reduced upper leaves, are 3-several branched above and have 3-several narrow discoid heads. In fact, the latter has nearly 20 heads. All are well within the limits of *A. discoidea* as circumscribed in the present study.

4. *Arnica gracilis* Rydb., Bull. Torrey Bot. Club 24:297. 1897. TYPE: Spanish Peaks (Madison Range, Montana), 6000 ft., July 14, 1896, *J.H. Flodman 901* (Holotype, NY!; Isotypes, NY!, US!) (Figure 22).

Arnica columbiana A. Nelson, Bot. Gaz. 30:200. 1900. TYPE: Columbia Falls, Montana, 1894, *J.J. Kennedy 24* (Holotype, MONT!).

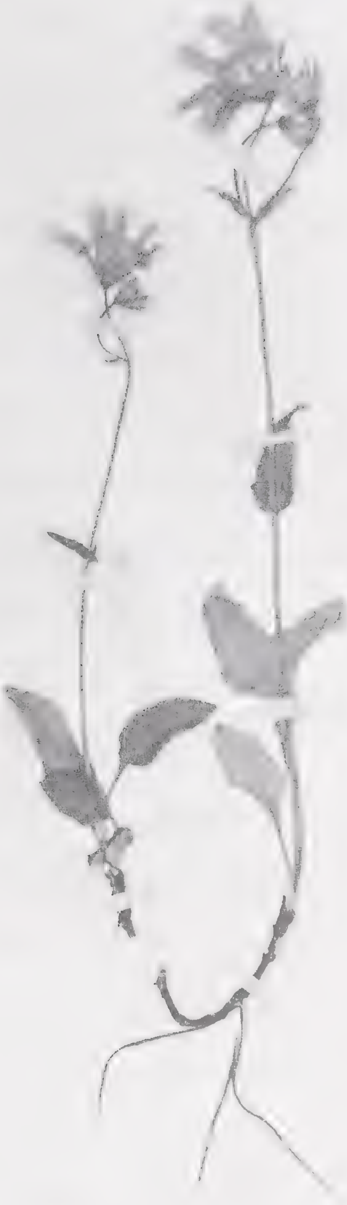
Arnica multiflora Greene, Pittonia 4:162. 1900. TYPE: Lake Pend d'Oreille, Idaho, June, 1891, *J.B. Leiberg 234* (Holotype, NDG).

Arnica lactucina Greene, Ottawa Nat. 23:214. 1910. TYPE: Hamilton Mt., Banff, Alberta, 5,800 ft., July 24, 1899, *W.C. McCalla 2014* (Holotype, US! Isotypes, CU photo!, NY!).

Arnica bentonicaefolia Greene var. *gracilis* (Rydb.) M.E. Jones, Bull. Univ. Mont. Biol. 15:48. 1910.

Arnica puberula Rydb., Fl. Rocky Mts. 979. 1917. TYPE: Head of Lake Louise, Alberta, July 22, 1904, *J. Macoun* (*Geol. Surv. Can. No. 65523*) (Holotype, NY!; Isotypes, CAN!, US!).

Figure 22. Holotype of _A_. _gracilis_ Rydb.



NEW YORK
BOTANICAL
GARDEN

MONOGRAPH OF THE GENUS ARNICA

Arnica gracilis Rydberg

Type!

NEW YORK BOTANICAL GARDEN
HERBARIUM OF DR. PER AXEL RYDBERG

Arnica latifolia Bong. var. gracilis (Rydb.) Cronquist, Vasc. Pl. Pac. NW 5:51. 1955.

Stems 3-several branched above, often in clumps of 5-10, 10-30 cm high, 1 mm diam., mostly short stipitate glandular above, becoming glabrate below; rhizomes 1-2 mm broad, covered with brown scales and old leaf bases; cauline leaves 2-3 pairs, ovate to ovate-lanceolate, 2-6 cm long, 1-3 cm broad, stipitate glandular above, glandular below, acute, irregularly serrate to sub-entire; petioles narrow to broadly winged, 1-6 cm long; upper pair of leaves often reduced and connate-perfoliate; leaves of the innovations 5-14, similar to cauline leaves but narrowly petiolate. Inflorescence a corymb of (3)5-15 heads or rarely a single head; penduncle 1.5-7 cm long, stipitate glandular, heads radiate, turbinate-campanulate, 10-15 mm high; involucral bracts 10-16, ovate-lanceolate, 6-12 mm long, 1-2 mm broad, short stipitate glandular, acute to acuminate. Ray florets 5-12, yellow, linear-elliptic, 10-20 mm long, 3-5 mm broad, 3-dentate; disc florets 10-25, yellow, tubular, 4-6 mm long, short stipitate glandular; pappus of both ray and disc florets white, barbellate. Achenes black, 4.5-7 mm long, 1 mm broad, short stipitate glandular with few duplex hairs. Chromosome number 2n = 57, 76.

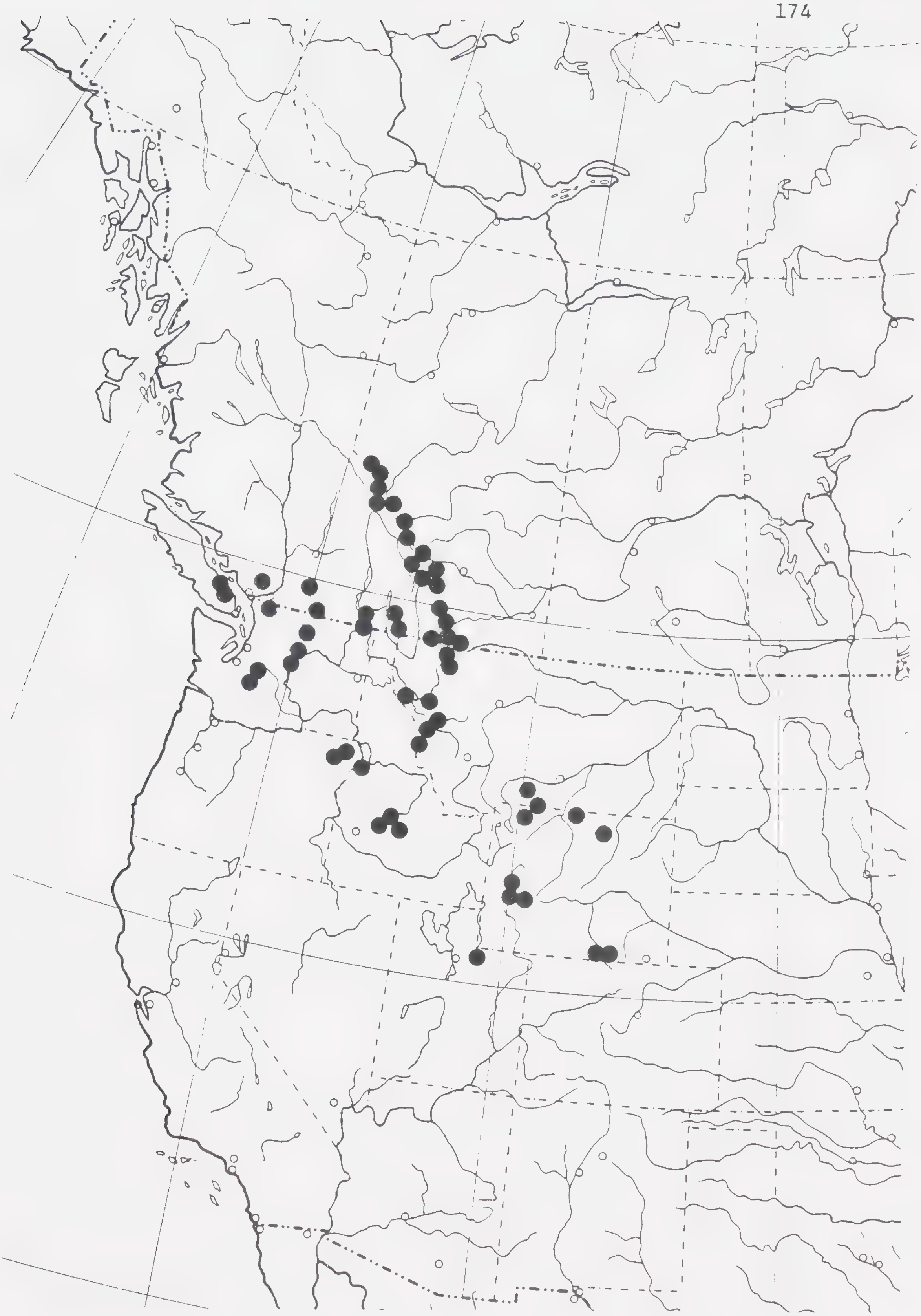
Ecology and Distribution: Relatively uncommon on dry, exposed, rocky, alpine slopes or occasionally sub-alpine forests in

the Rocky Mountains of Alberta, south irregularly to southern Wyoming, the Uintah Mountains of Utah, Wallowa Mountains of Oregon and infrequently in the Cascade Mountains of southern British Columbia south to Mt. Rainier, Washington. Also known from Vancouver Island (Figure 23). Elevational distribution from 1200-2500 m. Flowers July-August.

Arnica gracilis occurs on fairly exposed, rocky, alpine slopes or open sub-alpine forests (1200-2500 m) largely in the central Rocky Mountains. The close relationship of this taxon to *A. latifolia* has long been noted. Indeed, in his original description of *A. gracilis*, Rydberg (1897) noted it resembles a depauperate *A. latifolia*. Maguire (1943) considered *A. gracilis* a distinct species but called it "...a loose entity which is maintained as distinct from *A. latifolia* with some difficulty..." Cronquist (1955) and later Ediger and Barkely (1978) treated *A. gracilis* as a variety of *A. latifolia*, while Straley (1980) recently re-elavated it to specific status.

This confusion with *A. latifolia* is not surprising since the present study has clearly demonstrated that *A. gracilis* is a hybrid between *A. latifolia* and probably *A. cordifolia*. However, *A. gracilis* is readily separable from *A. latifolia* in several significant features including: broader, more numerous heads with broader phyllaries; the usually clumped habit; narrower, irregularly serrate to sub-entire, petiolate leaves; black achenes and the exposed, high altitude habitat (Table 4, see also Figure 25).

Figure 23. Distribution of *A. gracilis* Rydb.



According to Davis and Heywood (1963) the decision to give formal taxonomic recognition to hybrids depends on how common and morphologically distinct they are and how they behave in nature; i.e. whether they have "...become so stablized that they behave as species -- and have in fact become species..." *Arnica gracilis* is relatively common throughout the central Rocky Mountains, is morphologically quite distinct, and is an autonomous apomict that maintains itself quite vigorously in nature. As previously noted, populations of *A. gracilis* have been observed only a few meters from large populations of *A. latifolia* with no evidence of genetic mixing. The apomictic mode of reproduction, as well as the distinct ecology of this taxon has apparently severed all genetic ties to its parents. *Arnica gracilis* therefore "behaves" as a distinct species and is here recognized as such.

The type sheet of *A. gracilis* consists of 2 specimens, one with two heads and the other with three heads. Both have petiolate, irregulary serrate leaves and relatively broad heads with ovate-lanceolate phyllaries characteristic of this taxon.

Both the holotype and paratype (*R.S. Williams 1049*, Columbia Falls, Montana, June 14, 1894, RM) of *A. columbiana*, with numerous heads and long petiolate leaves are referable to *A. gracilis*.

The holotype of *A. multiflora*, examined and placed in synonymy with *A. gracilis* by Maguire (1943), is currently listed in the Greene Herbarium at Notre Dame University; however, it has not been located by the herbarium staff.

The holotype of A. lactucina as well as the two isotypes are rather large, but otherwise quite typical A. gracilis with numerous heads and irregularly serrate leaves.

The holotype of A. puberula as well as the two isotypes are somewhat intermediate between A. latifolia and A. gracilis. However, the narrowly petiolate leaves, branched habit, several broad heads with ovate-lanceolate phyllaries suggest a closer affinity with the latter. Arnica puberula is therefore placed in synonymy with A. gracilis.

Three taxa: A. jonesii, A. leptocaulis and A. bentonicaefolia; which have, at various times been included in the synonymy of A. gracilis, are here reduced to synonymy under A. latifolia. They will therefore be discussed under that species.

5. Arnica latifolia Bong., Mem. Acad. St. Petersb. VI 2:147. 1832. TYPE: Sitka, Alaska, Mertens s.n. (Lectotype by Maguire, LE photo!) (Figure 24).

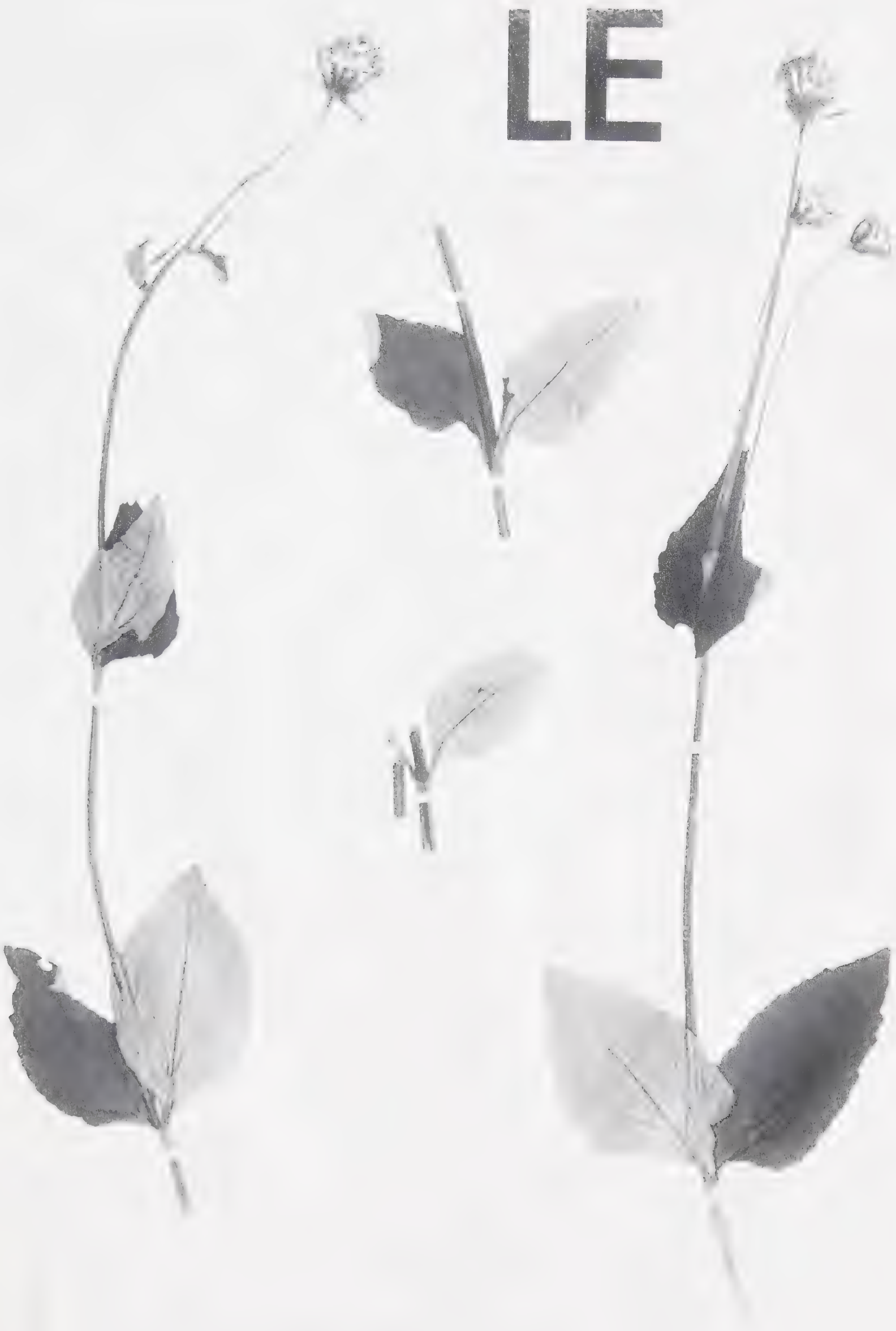
Arnica menziesii Hook., Fl. Bor. Am. 1:331. 1834. TYPE: Northwest coast of America, Menzies s.n. (Holotype: K photo!).

Arnica latifolia α genuina Herder, Bull. Soc. Nat. Mosc. 40:424. 1867. Based on A. latifolia Bong.

Arnica latifolia β angustifolia Herder, Bull. Soc. Nat. Mosc. 40:424. 1867. Based on A. menziesii Hook.

Arnica bentonicaefolia Greene, Pittonia 4:163. 1900. TYPE: Mt. Steele, Olympic Mountains, Washington, 6,000-7,000 ft., Aug., 1895, C.V. Piper 2002 (Holotype, NDG!; Isotype, GH!).

Figure 24. Holotype of _A_. _latifolia_ Bong.


LE

Arnica teucriifolia Greene, Pittonia 4:163. 1900. TYPE: grassy mountain slopes, divide between St. Joe and Clear Water River, alt. 1820 m, region of the Coeur d'Alene Mountains, Idaho, July 10, 1895, *J.B. Leiberg 1229* (Holotype, US!; Isotypes, MO!, NY!, POM!, UC!).

Arnica ovalifolia Greene, Pittonia 4:168. 1900. TYPE: Big Horn Mountains, Wyoming, 9,000-10,000 ft., July 17, 1890, *Blankinship s.n.* (Holotype, NDG!).

Arnica ventorum Greene, Pittonia 4:173. 1900. TYPE: Union Pass, Wind River Mountains, Wyoming, Aug. 11, 1894, *A. Nelson 836* (Holotype, NDG!, Isotypes, MO!, NY!, RM!, WS!).

Arnica grandifolia Greene, Pittonia 4:173. 1900. TYPE: Bridger Pass, Montana, July 28, 1896, *J.H. Flodman 896* (Holotype, NDG!; Isotypes, MO!, US!).

Arnica platyphylla A. Nelson, Bot. Gaz. 31:407. 1901. TYPE: moist dark Fir forests, Cascade Mts., Foothills, Hood River, Oregon, July 18, 1896 (Lectotype by Maguire, RM!).

Arnica laevigata Greene, Ottawa Nat. 15:279. 1902. TYPE: By springs in woods, Chilliwack Valley, B.C., alt. 3,000 ft., Aug. 5, 1901, *J.M. Macoun* (*Geol. Surv. Can. No. 26926*) (Holotype, NDG!; Isotypes, CAN!, NY!).

Arnica aprica Greene, Ottawa Nat. 15:280. 1902. TYPE: Open ground along streamlets, Chilliwack Valley, B.C., alt. 3,500 ft., July 10, 1901, *J.M. Macoun* (*Geol. Surv. Can. No. 26284*) (Holotype, NDG, photo UC!; Isotypes, CAN!, MO!, NY!).

Arnica jonesii Rydb., Fl. Rocky Mts., 979. 1917. TYPE: Alta, Wasatch Mountains, Utah, July 31, 1879, *M.E. Jones 1119* (Holotype, NY!: Isotypes, NY!, POM!, UTC!).

Arnica eriopoda Gandoger, Bull. Soc. Bot. Fr. 65:38. 1918. TYPE: Cascade Mountains, Oregon, July 27, 1902, *W.C. Cusick 2914* (Holotype US photo!; Isotypes, MO!, NY!, POM!, UC!).

Arnica aphanactis Piper, Proc. Biol. Soc. Wash. 33:105. 1920. TYPE: Mt. Baker, Washington, 1915, *G.W. Turesson s.n.* (Holotype, US!).

Arnica flodmanii Rydb., N. Am. Fl. 34:334. 1927. TYPE: Spanish Peaks, Madison Range, Montana, July 14, 1896, *J.H. Flodman 898* (Holotype, NY!; Isotypes, MO!, NY!, US!).

Arnica paucibracteata Rydb., N. Am. Fl. 34:336. 1927. TYPE: Medicine Bow Mountains, Wyoming, Aug. 3, 1900, *A. Nelson 7941* (Holotype, NY!; Isotypes, MO!, POM!, RM!, US!).

Arnica oligolepis Rydb., N. Am. Fl. 34:336. 1927. TYPE: Hazelton, Skeena River, B.C., June 23, 1917, *J.M. Macoun* (*Geol. Surv. Can. No. 96048*) (Holotype, NY!: Isotype, CAN!).

Arnica leptocaulis Rydb., N. Am. Fl. 34:336. 1927. TYPE: Mt. Mark, Vancouver Island, B.C., July 25, 1887, *J.M. Macoun s.n.* (Holotype, NY!, Isotypes, CAN!, US!).

Arnica membranacea Rydb., N. Am. Fl. 34:338. 1927. TYPE: Wimmer, Jackson Co., Oregon, June 13, 1892, *E.W. Hammond 231* (Holotype, NY!; Isotypes, US!, WS!).

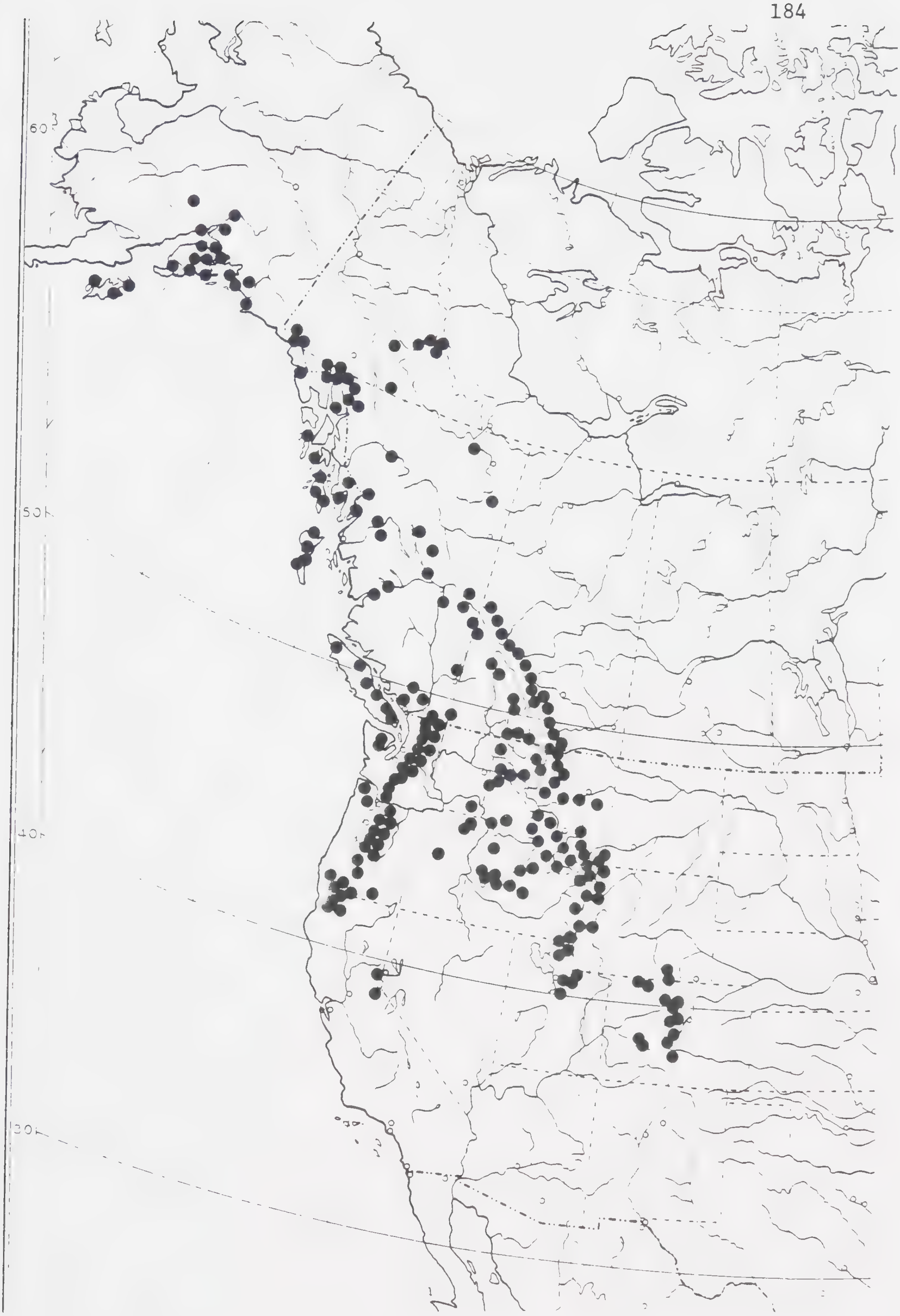
Arnica latifolia Bong, var. teucriifolia (Greene) L. Williams, Leafl. West. Bot. 1:171. 1935.

Stems simple, sometimes sparsely branched above, 10-50 cm high, 2-3 mm diam., glabrate to villous throughout; rhizomes 1-3 mm thick, giving rise to several basal rosettes and flowering stems, rhizomes with several thin brown scales, frequently covered with old leaf bases at the summit. Cauline leaves 2-4(6) pairs, mostly sessile to sub-sessile, the lower rarely petiolate, ovate to elliptic-lanceolate, 2-10 cm long, 1-6 cm broad, glabrous to very sparsely villous, obtuse to acute, serrate to dentate; lower leaves often reduced and short petiolate, the petioles 5-15 mm long, broadly winged; leaves of the innovations 2-10, similar to cauline leaves, petiolate, the petioles 2-10 cm long. Inflorescence usually a single head or corymb of 3-5(9) heads; peduncle 3-25 cm long, glabrate to sparsely villous above; heads radiate, narrowly turbinate, 8-20 mm high; involucral bracts 8-20, lanceolate to oblanceolate, 8-15 mm long, 1-3 mm broad, sparsely villous and glandular, acute to acuminate. Ray florets 8-15, yellow, oblong-linear, 10-25 mm long, 2-6 mm broad, 3-dentate; disc florets 20-90, yellow, tubular, 6-10 mm long, sparsely villous; pappus of both ray and disc florets white, barbellate. Achenes dark brown, 5-9 mm long, 1 mm broad, sparsely short stipitate glandular with few duplex hairs. $2\underline{n} = 38, 76$.

Ecology and Distribution: Common in relatively moist, montane *Picea* - *Abies* forests, or more commonly sub-alpine meadows from southern interior and coastal Alaska south along the coast and through the Cascades to northern California, and south in the Rocky Mountains from the Yukon through southern Colorado. Also common on Vancouver Island and the Queen Charlotte Islands (Figure 25). Elevational distribution from 500-3300 m. Flowers July-August.

Arnica latifolia is one of the most polymorphic and widely distributed of western arnicas. This taxon is common in relatively cool, montane *Picea* - *Abies* forests or sub-alpine meadows from Alaska through Colorado and northern California. In its most typical form *A. latifolia* is easily recognized by its sessile, ovate, glabrous leaves; very narrow heads with narrow phyllaries and rays; and glabrous, brown achenes. However, both environmentally induced morphological variability and plants with petiolate lower cauline leaves are not infrequently encountered. Consequently, this taxon has frequently been confused with both *A. cordifolia* and *A. gracilis*. Plants of shaded forests represent the typical form of the species while plants of more exposed areas are usually much reduced; have thicker, smaller, more glandular leaves; have broader heads with more glandular phyllaries and are often confused with *A. gracilis*. However, they are readily separable from the latter by their broader, sessile, petiolate leaves and fewer heads. Pressed specimens of *A. latifolia* with petiolate lower leaves are

Figure 25. Distribution of _A_. _latifolia_ Bong.


60
50
40
30

sometimes confused with A. cordifolia, but can usually be distinguished by leaf shape and margin and by several characters of the fruits and inflorescence (see Table 4, page 37).

As previously noted, A. latifolia was probably derived, in wetter sites, from ancient diploid populations of A. cordifolia. Although hybridization between the two species, which probably produced A. gracilis, seems to have taken place in the past, there appears to have been little mixing since. Populations of A. cordifolia are often encountered near populations of A. latifolia and the two species sometimes grow intermixed. Despite extensive searching of two such intermixed populations (S. Wolf 397, 398 ALTA Blind Stream Rd., Duchense Co., Utah and S. Wolf 367, 368, near Swauk Pass, Chelan Co., Washington, ALTA) no evidence of hybridization between the two species could be detected. In both populations the A. latifolia was diploid while the A. cordifolia was tetraploid. The subsequent development of polyploidy and apomixis in A. cordifolia has evidently prevented genetic mixing between the two taxa in more recent times.

The lectotype of A. latifolia, selected by Maguire, consists of two flowering shoots and three fragments of leaves and stems. All have ovate, serrate, sessile to sub-sessile leaves typical of A. latifolia.

The type sheet of A. menziesii consists of three specimens, two of which represent the holotype collected by Menzies. Both are referable to A. latifolia. The third specimen; collected by Tolmie s.n. at Mt. Rainier Washington is also A. latifolia.

Herder (1867) treated A. menziesii as A. latifolia β angustifolia and the Sitka collection of Mertens as A. latifolia α genuina.

The type sheet of A. betonicaefolia consists of two collections: C.V. Piper 2202 and 2002. Both were collected on Mt. Steele, Washington, in August, 1895; however, the former was collected at 7,000 ft. while the latter was collected at 6,000 ft. Maguire (1943) reduced A. bentonicaefolia to synonymy under A. latifolia and cited 2002 as the holotype while Ediger and Barkley (1978), who reduced this taxon under A. gracilis, cited 2202. Both collections represent the reduced high alpine form of A. latifolia and have ovate, serrate, sessile leaves and solitary narrow heads typical of this taxon. There is really no question as to which collection represents the holotype of A. betonicaefolia since Greene (1900), in his original protologue clearly designated 2002.

The holotype sheet of A. teucriifolia consists of five flowering shoots and two sets of basal rosettes. It represents fine examples of typical A. latifolia with ovate, sessile to sub-sessile cauline leaves, solitary heads and long petiolate innovations.

The type sheet of A. ovalifolia consists of two specimens and represents a mixed collection. The specimen on the right is A. latifolia while the specimen on the left is A. mollis Hook.

Both the holotypes and all isotypes of A. ventorum and A.. laevigata, as well as the lectotype of A. platyphylla, are all very typical specimens of A. latifolia.

Arnica grandifolia represents a mixed collection with an isotype at NY being *A. cordifolia* while the remaining isotypes (MO, US) and holotype (NDG) are all *A. latifolia*. Indeed, Rydberg had originally labelled the NY sheet as *A. cordifolia* but later changed the name on the sheet to *A. grandifolia*. However, since the holotype is referable to *A. latifolia*, *A. grandifolia* is here reduced to synonymy under that species.

The holotype of *A. aprica* is currently listed in the Green Herbarium at Notre Dame University but has not been located. However, a photo of this specimen from the University of California at Berkley, as well as the three isotypes examined, have demonstrated that this taxon represents a very typical form of *A. latifolia*.

Ediger and Barkley (1978) reduced *A. jonesii* to synonymy under *A. gracilis* . However, the holotype as well as the isotypes represent very typical *A. latifolia* with broadly, ovate, serrate to dentate, sessile leaves.

According to Maguire (1943), the holotype of *A. eriopoda* is located at the U.S. National Herbarium; however, this specimen has not been subsequently located. An early photo of this specimen at the University of California, Berkeley, as well as four isotypes have been examined. All represent very typical *A. latifolia*. Likewise, the holotype of *A. aphanactis* represents a typical *A. latifolia* with broad, ovate, sessile upper leaves with the lower pair short petiolate.

The types of *A. flodmanii*, *A. glabrata*, *A. paucibracteata*, *A. oligolepis*, *A. leptocaulis* and *A. membranacea*; all described in his Flora of North America (1927), clearly illustrate Rydberg's failure to recognize natural variability and his proclivity for "splitting." Rydberg delimited these taxa by their overall stature, leaf length, number of phyllaries and whether the lower leaves were sessile or petiolate. Indeed, with the exception of the latter, all these characteristics are quite variable in virtually any plant species; particularly the highly polymorphic *A. latifolia*.

Four taxa which have, at various times, been placed in synonymy with *A. latifolia* are here rejected. *Arnica granulifera* Rydb., Fl. Rocky Mts., 978. 1917. TYPE: Long Baldy, Little Belt Mt., Montana, Aug, 19, 1896, *J.H. Flodman s.n.* (Holotype, NY!) is *A. mollis* and can be recognized by its broad heads with broad phyllaries and dark, plumose pappus.

Arnica latifolia Bong. var. *visidula* A. Gray, Syn. Fl. N. Am. 1:381. 1884. TYPE: Sierra Nevada Mts., California, Sept. 25, 1882, *C.G. Pringle 2* (Holotype, US!) is *A. diversifola* Greene and can be recognized by its coarsely, petiolate leaves and broad heads with dark, plumose pappus.

Both *A. lactucina* Greene and *A. puberula* Rydb. are referable to *A. gracilis* and have previously been discussed under that taxon.

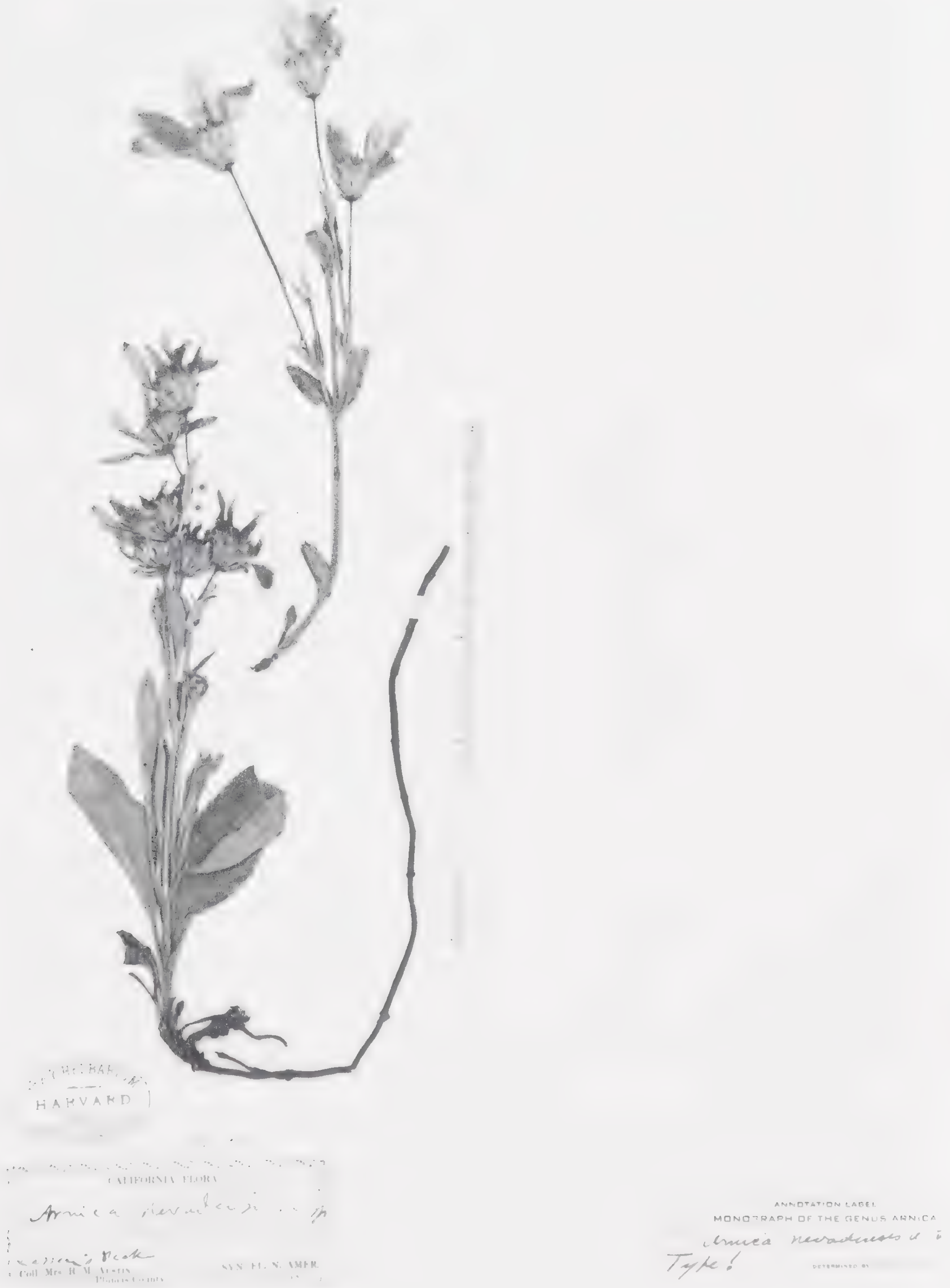
6. *Arnica nevadensis* A. Gray, Proc. Am. Acad. 19:55. 1883. TYPE: Lassen's Peak, California, *R.M. Austin s.n.* (Lectotype by

Rydberg, GH! (Figure 26); Syntype, Summit Valley, California, Sept. 25, 1882, C.G. Pringle s.n. (NY!).

Arnica tomentella Greene, Pittonia 4:166. 1900. TYPE: open woods in Middle Tule River, California, alt. 5500 ft., April-Sept. 1897, C.A. Purpus 5625 (Holotype, US!; Isotypes, GH!, MO!, UC!).

Stems simple, 10-50 cm high, 1.5-2.5 mm diam., short stipitate glandular throughout and puberulent above, rhizomes 1-2 mm thick, with several brown scales and old leaf bases at the summit. Cauline leaves 2-3 pairs, ovate to elliptic, 3-8 cm long, 2-4 cm broad, short stipitate glandular throughout, acute to rounded, entire to denticulate; petioles narrow to broadly winged, 1.5-4.0 cm long; upper pair of leaves often reduced, sessile and lanceolate; leaves of the innovations 4-6, similar to cauline leaves. Inflorescence a single head or corymb of 3 heads; peduncle 4-15 cm long, stipitate glandular and somewhat villous; heads radiate, campanulate-turbinate, 15-20 mm high; involucral bracts 10-16, oblanceolate, 10-17 mm long, 2-4 mm broad, stipitate glandular, acute to acuminate. Ray florets 6-14, yellow, linear to broadly elliptic, 15-25 mm long, 4-6 mm broad, 3-dentate; disc florets 20-60, yellow, tubular, 8-10 mm long, short stipitate glandular; pappus of both ray and disc florets white to tawny, barbellate to subplumose. Achenes dark grey, 6-9 mm long, 1 mm broad, stipitate glandular throughout. Chromosome number $2n = 76$.

Figure 26. Holotype of A. nevadensis A. Gray.



HARVARD

CALIFORNIA FLORA

Arnica nevadensis n. sp.

Castle's Peak
Coll. Mrs. R. M. Austin
Plumas County

SYN. FL. N. AMER.

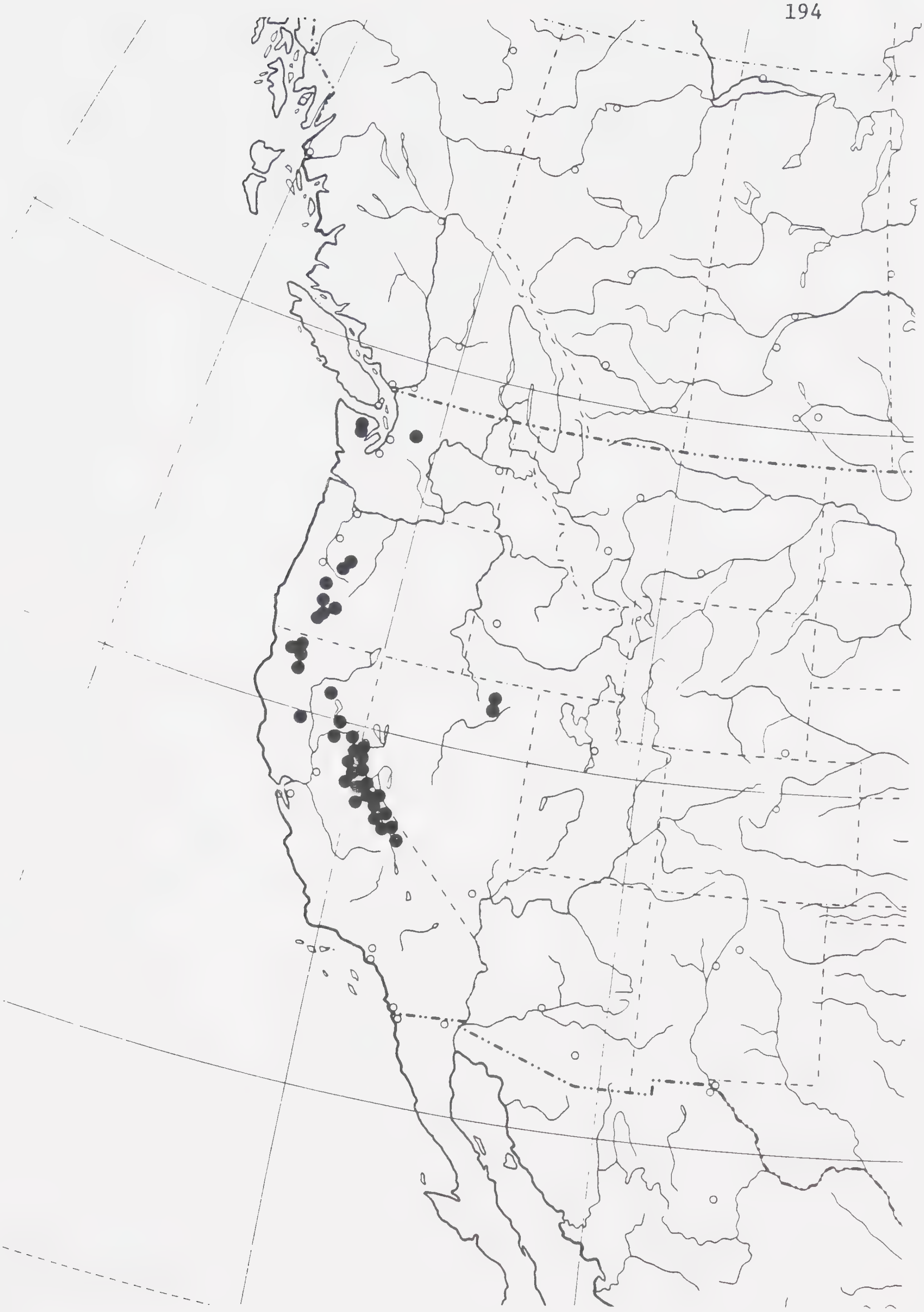
ANNOTATION LABEL
MONOGRAPH OF THE GENUS ARNICA
Arnica nevadensis
Type!
DETERMINED BY

Ecology and Distribution: Relatively uncommon in fairly dry *Tsuga* - *Pinus* forests or exposed rocky slopes of the Sierra Nevada Mountains from south of Yosemite National Park, California and adjacent Nevada, northward irregularly to the north Cascades and Olympic Mountains of Washington. Also known from the Ruby Mountains of Nevada (Figure 27). Elevational distribution 1500-3500 m. Flowers July-August.

Arnica nevadensis occurs mostly at high elevations (1500-3500m) in open *Tsuga* - *Pinus* forests or open rocky slopes of the Sierra Nevada and sparingly northward in the Cascades and eastward into Nevada. In the southern part of its range this taxon is quite distinct and readily recognized by its entire, elliptic to ovate leaves; oblanceolate phyllaries; white-tawny, barbellate-subplumose pappus and relatively open, high altitude habitat. However, in the northern part of its range it is often confused with dwarf, high altitude forms of *A. cordifolia*. This is not surprising since, as previously noted, *A. nevadensis* is probably derived, at least in part, from *A. cordifolia*. However, the entire leaves, darker pappus with longer seta and narrower heads of *A. nevadensis* distinguish it from the latter.

In his original description of *A. nevadensis* Gray (1883) did not designate a type, however he cited two specimens he had examined: *R.M. Austin s.n.*, Lassen's Peak, California (GH) and *C.G. Pringle s.n.*, Summit Valley, California (NY). In his Flora of

Figure 27. Distribution of _A_. _nevadensis_ A. Gray.



North America, Rydberg (1927) designated the first specimen cited (Austin) as the lectotype for this taxon. This choice was also later accepted by Maguire (1943). However, recently Ediger and Barkely (1978) rejected Rydberg's choice as arbitrary and designated the second specimen cited (Pringle) as the lectotype "...in order to preserve the traditional application of the name." According to the rules of the International Code of Botanical Nomenclature (Stafleu et al, 1978) this practice cannot be accepted without proper justification. Both article 8 and the Guide of the Determination of Types specifically state that the first choice of a lectotype must be followed by subsequent workers unless it can be shown that the choice was based on a misinterpretation of the protologue or if the choice was made arbitrarily and without understanding the group concerned.

Ediger and Barkley (1978) based their decision on Recommendation 7B which states "Whenever the elements on which the name of a taxon is based are heterogeneous, the lectotype should be so selected as to preserve current usage..." Although poorly pressed; the ovate, entire leaves as well as the broad rays and tawny, subplumose pappus of the Austin specimen are typical of A. nevadensis. Further, it seems clear that Gray's (1883) description was based on the Austin specimen. He made specific reference to the cinereous color in both the type description and the discussion of the Austin specimen, while noting that the Pringle specimen was a "greener form." Although Rydberg (1927) gave no reason for his

choice of the Austin specimen at the Gray Herbarium, he must have given it close examination since it would have been much easier for him to cite the Pringle specimen at the New York Botanical Garden. Rollins (1972) has stressed the importance of selecting a lectotype from the institution where the author worked. Since both specimens cited by Gray (1883) are referable to A. nevadensis, but the first cited (Austin, GH) was originally chosen as lectotype by Rydberg (1927), it must be retained as the lectotype for this taxon.

Both Maguire (1943) and Ediger and Barkley (1978) recognized the rare A. tomentella of the Sierra Nevada, while Straley (1980) tentatively placed this taxon in synonymy with A. nevadensis. Maguire (1943) considered A. tomentella a close relative of A. nevadensis. Indeed, even a casual comparison of his (Maguire, 1943) description of the two taxa indicates they are nearly identical in most respects including: stem pubescence, leaf shape and margin, head shape, phyllary and ligule shape and all characters of the pappus. Only the taller stature and tuft of hairs on the phyllary tips distinguish A. tomentella from A. nevadensis. Coincidentally, both Gray (1883) and Greene (1900) in their original descriptions of these two taxa noted the cinereous color and resemblance of their taxa to Whitneya dealbata A. Gray.

Straley (1980) has shown A. nevadensis to be entirely apomictic. Arnica tomentella may represent an apomictic microspecies of A. nevadensis or more likely an environmentally induced form of the latter. Nevertheless, it is not considered either morphologically

or geographically distinct enough to receive taxonomic recognition. Here, it is therefore reduced to synonymy with A. nevadensis.

Three specimens (J.P. Tracy 19273 UC, C.F. Sonne s.n. UC #193450 and G.D. Butler 643 UC) previously recognized as A. tomentella are A. cordifolia. Other specimens previously recognized as A. tomentella (Lemmon s.n. UC #337194; C.F. Sonne s.n., June 6, 1886 GH, UC; C.A. Purpus 1540 UC; T.S. Brandegee s.n. UC #91026; C.A. Purpus 5625 GH, MO, UC, US) are all treated here as A. nevadensis. Another collection previously identified as A. tomentella (Bolander 4937 UC) is A. mollis Hook.

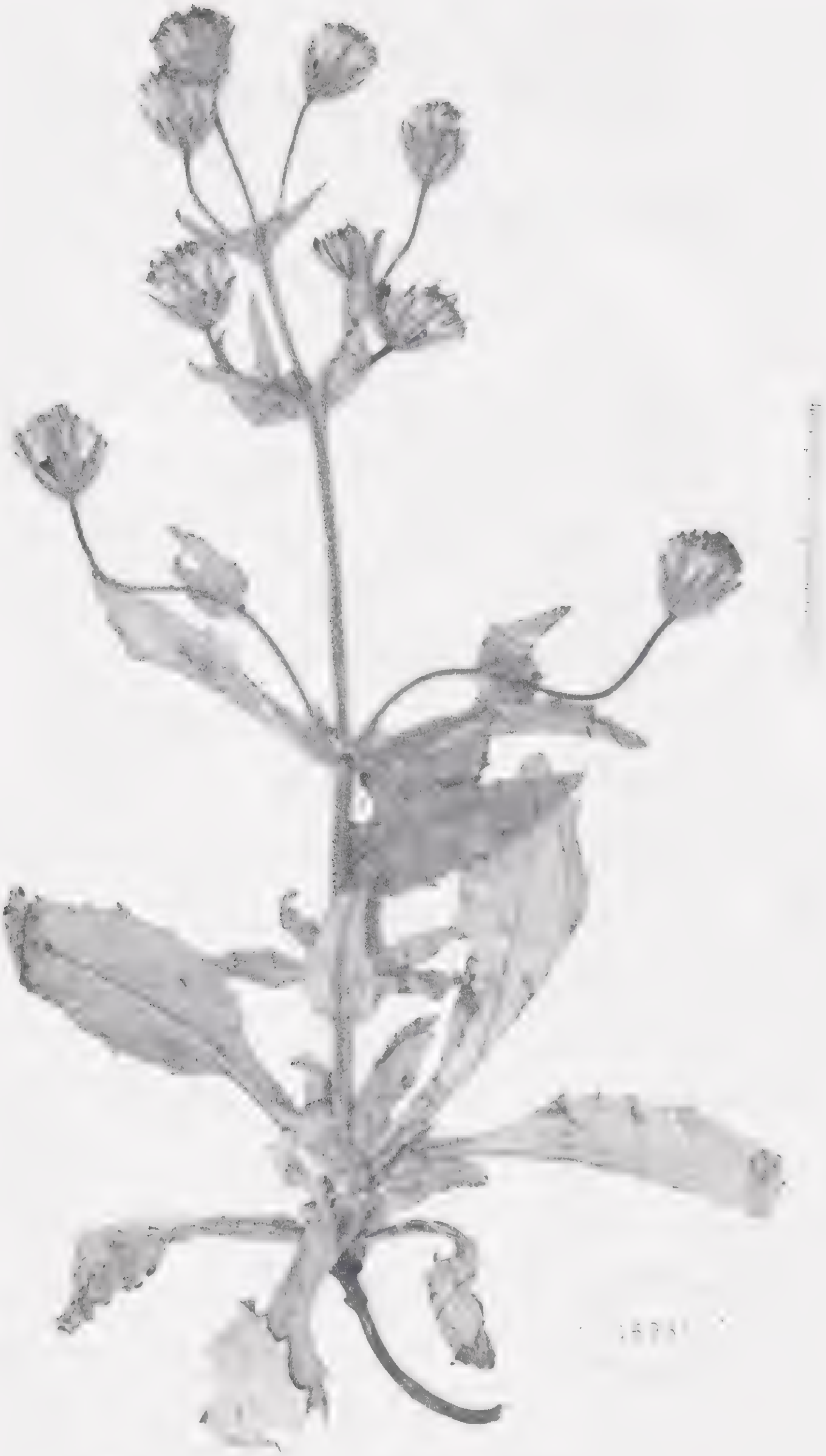
Although the type specimen of A. chionophila was not seen by either Maguire (1943) or Straley (1980), both placed this taxon in synonymy with A. nevadensis. However, as previously noted under A. cordifolia, this epithet merely represents a dwarf form of that taxon.

7. Arnica spathulata Greene, Pittonia 3:103. 1896. TYPE: Glendale, Oregon, June 30, 1887, T. Howell s.n. (Holotype, NDG!; Isotypes, CAN!, US!) (Figure 28).

Arnica eastwoodiae Rydb., N. Am. Fl. 34:343. 1927. TYPE: Gasquet, French Hill, Del Norte Co., California, Sept. 14, 1912, A. Eastwood 2211 (Holotype, NY!; Isotypes, NY!, US!).

Arnica cusickii Rydb., N. Am. Fl. 34:343. 1927. TYPE: Dry western slopes, Cascade Mountains, southern Oregon, July 11, 1902, W.C. Cusick 2873 (Holotype, NY!; Isotypes, MO!, ORE!, POM!, UC!, US!).

Figure 28. Holotype of _A_. _spathulata_ Greene.



Arnica *spathulata* Greene subsp. *eastwoodiae* (Rydb.) Maguire, Brittonia 4:458. 1943.

Arnica *spathulata* Greene var. *eastwoodiae* (Rydb.) Ediger and Barkley. N. Am. Fl. II. 10:43. 1978.

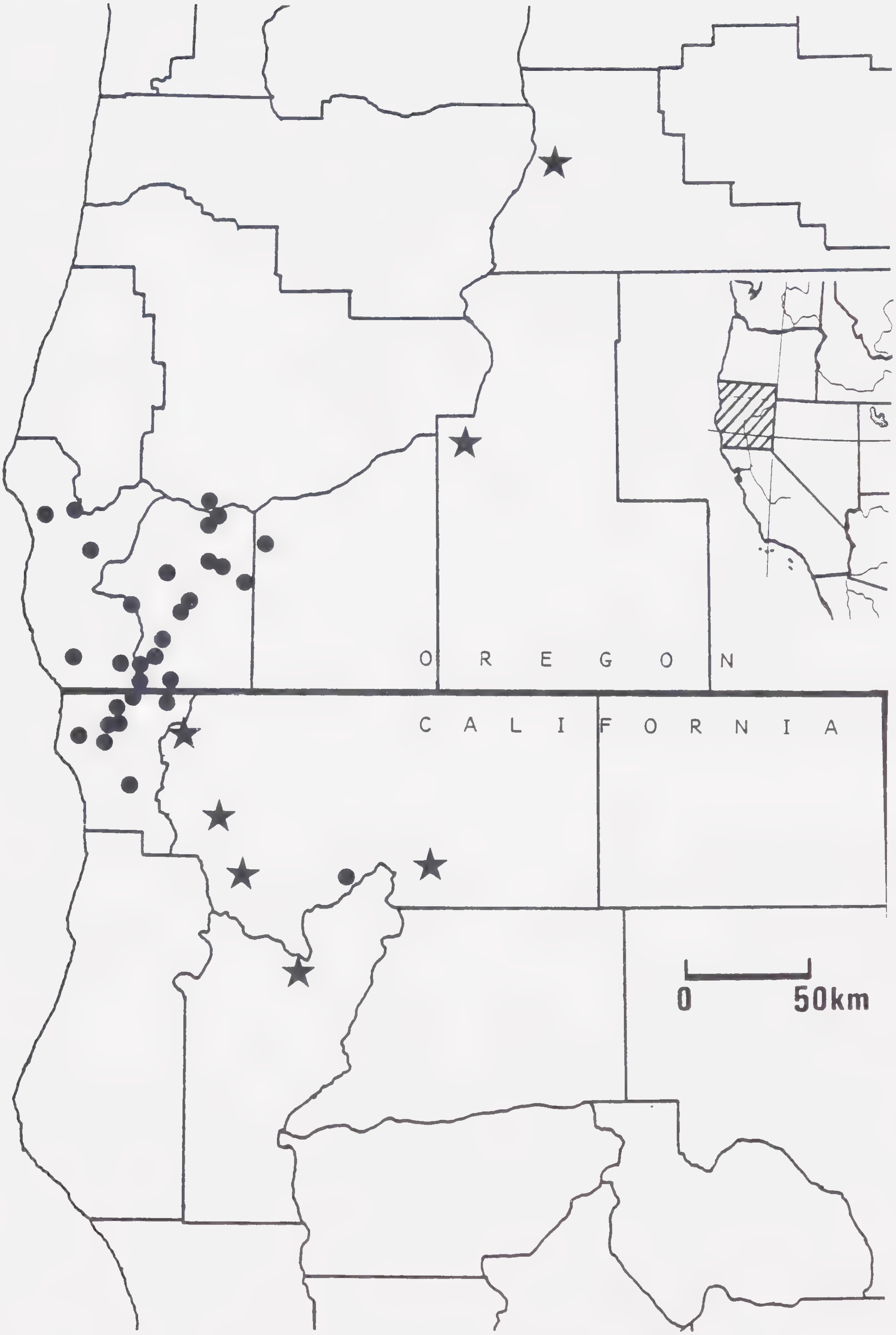
Stems simple to several branched, 15-50 cm high, 2-3 mm diam., sparsely to densely villous and stipitate glandular throughout; rhizomes giving rise to several basal rosettes and flowering stems, 2-3 mm thick, covered with scales and old leaf bases at the summit. Cauline leaves 3-5 pairs, sometimes crowded towards stem base and reduced above, spathulate to elliptic-ovate, 2-8 cm long, 1-4 cm broad, sparsely to densely villous and stipitate glandular, acute, subentire to mostly irregularly dentate; petioles mostly broadly winged, 1-9 cm long, 2-15 mm broad; leaves of the innovations 4-10, similar to cauline leaves. Inflorescence a solitary head or corymb of 3-9(25) heads; peduncles 2-20 cm long, sparsely to densely villous and long stipitate glandular; heads discoid, turbinate-campanulate, 15-28 mm high; involucral bracts 8-15, broadly to narrowly lanceolate, 5-15 mm long, 1-4 mm broad, sparsely to densely villous and stipitate glandular, acute to obtuse. Florets 15-50, yellow, tubular, 8-11 mm long, sparsely villous and glandular below; pappus white, barbellate. Achenes black, 5-10 mm long, 1 mm broad, sparsely short stipitate glandular. Chromosome number $2\underline{n} = 38, 76$.

Ecology and Distribution: Very rare and forming relatively small populations in dry, open Pinus - Quercus - Pseudotsuga menziesii forests or such disturbed areas as roadcuts. Largely restricted to serpentine soils in Curry, Douglas, Jackson and Josephine Counties, Oregon and Del Norte and Siskiyou Counties, California (Figure 29). Elevational distribution 200-1500m. Flowers April-July.

Arnica spathulata is a relatively rare, predominantly serpentine endemic, and occurs in open Pinus forests at mid elevations (200-1500 m) in the Coast Ranges of the Klamath region. As previously noted, this taxon is almost certainly derived from A. discoidea. However, it is readily distinguished by its spathulate, broadly winged, petiolate leaves; broader phyllaries and larger, black achenes which lack duplex hairs.

In more exposed habitats specimens of A. spathulata are often smaller, less hairy, with narrower, frequently reddish leaves crowded towards the base. Plants with this habit have previously been recognized as A. eastwoodiae by Rydberg (1927). Maguire (1943) tentatively recognized this taxon as a subspecies of A. spathulata but noted it may in fact only represent an environmentally reduced form. As previously noted, these characters are probably environmentally induced and no correlations between morphology, chromosome number, geography or flavonoid chemistry could be discerned in this form. Therefore it has not received formal taxonomic recognition in the present study.

Figure 29. Distribution of *A. spathulata* Greene (●) and *A. viscosa* A. Gray (★).


OREGON
CALIFORNIA
0
50km

In his original description of *A. spathulata* Greene (1896) did not designate a type or refer to any specimens examined. Maguire (1943) later designated a Howell specimen at the U.S. National Herbarium as the lectotype for this taxon (*T. Howell s.n.* Glendale, Oregon, June 30, 1887 (erroneously cited by Maguire as June 3)). However, a specimen of *A. spathulata* on which Greene had written "Actual type of my *A. spathulata*, Pitt. iii. 103!" (Figure 28) has been located in his personal herbarium at Notre Dame University. According to Article 8 of the International Code of Botanical Nomenclature (Stafleu *et al*, 1978) this specimen supercedes Maguire's (1943) lectotype and is here treated as the holotype of *A. spathulata*. Both the U.S. National Herbarium specimen, previously chosen as lectotype, as well as a specimen at the National Museum of Canada are of the same collection as the holotype and are here recognized as isotypes.

The holotype of *A. spathulata* consists of one specimen with reddish, spathulate, broadly petiolate leaves mostly crowded towards the base and nine heads typical of this taxon.

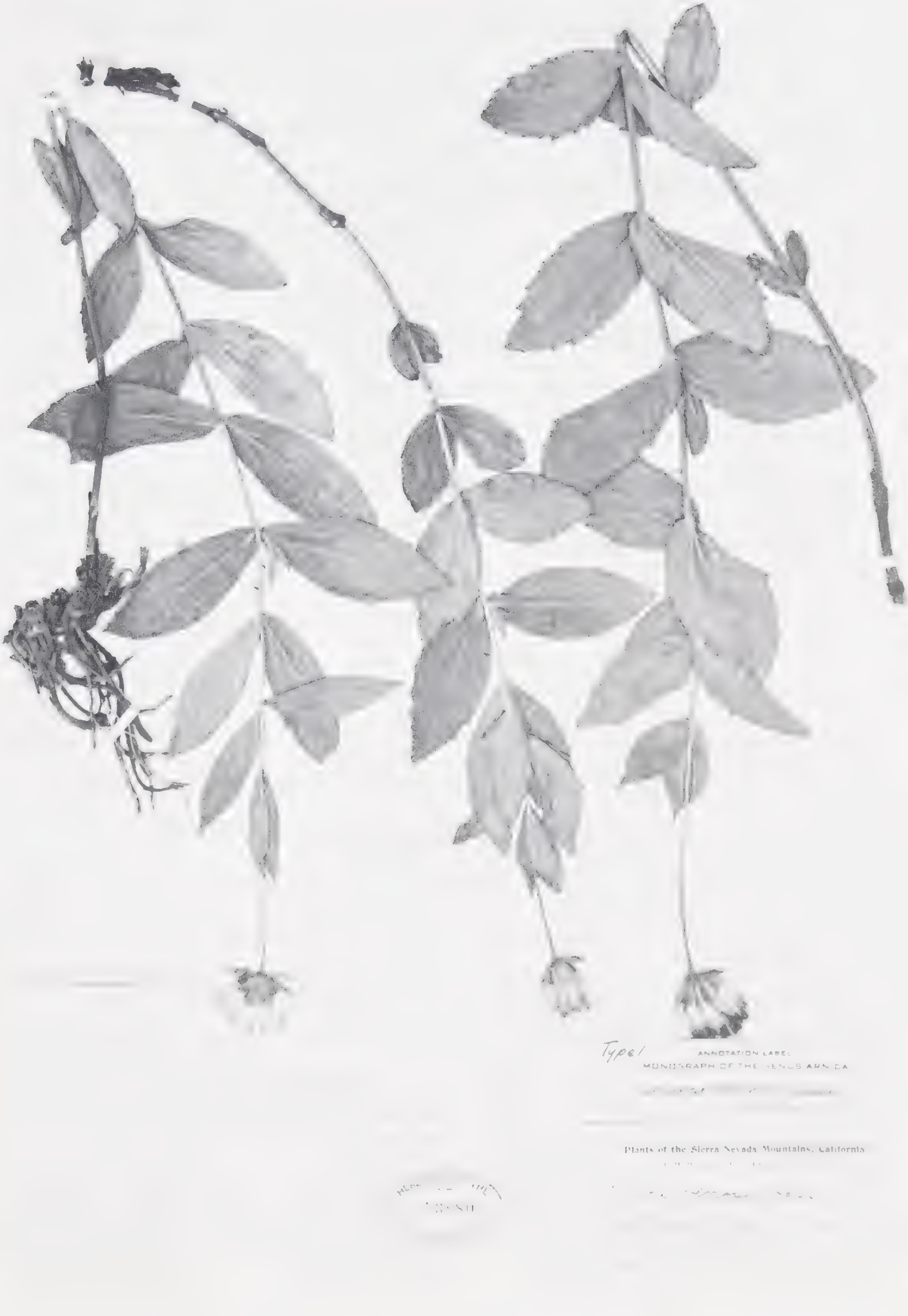
The holotype of *A. eastwoodiae* consists of two specimens with narrower and less pubescent leaves characteristic of the exposed form of *A. spathulata*. However, the isotype of this taxon at the New York Botanical Garden consists of two plants one of which resembles the holotype while the other has broader, spathulate leaves more characteristic of *A. spathulata*.

The holotype of *A. cusickii* consists of two plants, one of which represents a very typical *A. spathulata* in both leaf and inflorescence characters. The other specimen has less spathulate leaves with narrower petioles but it otherwise referable to *A. spathulata*.

8. *Arnica venosa* H.M. Hall, Univ. Calif. Pub. Bot. 6:174. 1915. TYPE: Salt Creek, Shasta Co., California, alt. 430 m. *H.M. Hall and E.B. Babcock 4013* (Holotype, UC!; Isotypes, GH!, NY!, RM!, UC!, US!) (Figure 30).

Stems simple to 3-several branched, prominently ribbed, 20-60 cm high, 2-5 mm diam., densely pilose and stipitate glandular above to less so below; woody caudex 3-5 mm broad, covered with dark scales and old leaf bases. Lacking basal rosettes; cauline leaves 6-10 pairs, the middle largest, becoming reduced and bract-like above and scale-like below, broadly sessile or rarely short-broadly petiolate, ovate-elliptic to broadly lancelate, 3-7 cm long, 1.5-4 cm broad, firm, 3-5 nerved above, strongly reticulate-veined below, glabrate to stipitate glandular above, pilose and stipitate glandular below, especially on veins below, acute to obtuse, irregularly and coarsely serrate. Inflorescence a solitary head on each branch, 1-7; peduncle 2-5 cm long, densely pilose and stipitate glandular toward summit; heads discoid, turbinate-campanulate, 15-22 mm high; involucral bracts 8-19, 8-16 mm long, 3-5 mm broad,

Figure 30. Holotype of _A_. _venosa_ H. M. Hall.


Type!
ANNOTATION LABEL
MONOGRAPH OF THE GENUS ARNICA
Plants of the Sierra Nevada Mountains, California

ovate to broadly lanceolate, pilose and stipitate glandular, acute to obtuse. Florets 30-60, yellow, tubular, 8-10 mm long, densely pilose below; pappus white, barbellate. Achenes dark grey, angled and ribbed, 6-8 mm long, 1.5 mm broad, densely hirsute with duplex hairs. Chromosome number $2n = 38$.

Ecology and Distribution: A very rare species of very dry, open *Pinus* - *Quercus* forests or, more commonly, such disturbed sites as road cuts. Known from about 20 small populations, largely in western Shasta County and adjacent Trinity County, California (Figure 17). Elevational distribution 400-1400 m. Flowers May-June.

Arnica venosa is probably one of the rarest and most geographically restricted species of *Arnica*. It is known from about 20 populations, all within a 25 km radius, largely in western Shasta County, California. It is restricted largely to north facing slopes, at elevations of 400-1400 m, in open *Pinus* - *Quercus* forests or more commonly on such disturbed sites as road cuts. Until very recently *A. venosa* was known from only six populations and, consequently, appeared on the California list of rare and endangered species (Smith *et al*, 1980). However, based largely on the efforts of Ms. Barbara Williams of the Shasta-Trinity National Forest, considerably more populations have recently been discovered. The present author is greatly indebted to Ms. Williams for

providing considerable informaton on A. venosa including both herbarium specimens and very detailed and complete ecological observations.

In its typical form A. venosa is readily recognized by its rather stout, leafy stem; woody caudex; absence of innovations and broadly sessile, ovate-elliptic, reticulate-veined, coarsely dentate, very firm leaves. Since few specimens were available for examination, previous studies have concluded that this taxon exhibits little variability (cf Straley, 1980). However, the availability of and study of many newly collected specimens has revealed that A. venosa, like most other Austromontana species, exhibits considerable morphological variablity and appears to intergrade into A. discoidea. As previously noted, this taxon is probably derived from A. discoidea. At one extreme are typical forms of A. venosa with leafy stems and broadly sessile, veined leaves such as the type collection Hall and Babcock 4013 (GH, NY, RM, UC, and US); S.J. Wolf 468, 469 (ALTA) and B.L. Williams 251 (STNF). At the other extreme are such specimens as B.L. Williams 371 (STNF) with weakly veined, long, narrowly petiolate leaves more characteristic of A. discoidea. This specimen is an otherwise typical form of A. venosa and is characteristically highly branched above with very reduced leaves. Additionally, this specimen was collected near a population of A. discoidea and may represent some introgression from that species. However, without further evidence a hybrid hypothesis would be difficult to support. Another seemingly in-

termediate form is represented by B.L. Williams 250 (STNF) which has very typical upper leaves, leafy stems and floral characters but has narrowly petiolate leaves below the mid-stem.

Whether these seemingly intermediate forms represent introgression between *A. discoidea* and *A. venosa* or natural variability in the latter is unclear. It is clear, however, that these two species are more similar than previously demonstrated. *A. venosa* differs from *A. discoidea* largely by its sessile leaves, woody caudex and lack of basal rosettes. However, the present study has demonstrated that the character of sessile leaves represents only one point on a continuum between narrowly petiolate and sessile leaves. The two characters of woody caudex and lack of basal rosettes may in fact be only one character, with the latter a consequence of the former. In addition, in several species of *Arnica* such as *A. longifolia* D.C. Eaton, *A. mollis* Hook. and *A. acaulis* (Walt.) Britton; the rhizomes are frequently shortened into a thick caudex (Ediger and Barkley, 1978). Some specimens of *A. venosa* (B.L. Williams 371, STNF) possess a thin, slightly woody caudex which is barely distinguishable from a rhizome.

Arnica venosa was most likely originally a fire species which colonized recently burned areas (B.L. Williams, pers. comm.). With the advent of strict fire control in more recent times this taxon is now largely restricted to such recently disturbed sites as road cuts. The similar flavonoid profiles and morphology between *A. discoidea* and *A. venosa* as well as the very restricted distribution

and preference for disturbed habitats of the latter suggests it was derived from the former, probably in relatively recent times. The woody caudex and concomitant lack of basal rosettes in A. venosa may in fact be an adaptation to its disturbed habitat and/or relatively hot, dry habitat.

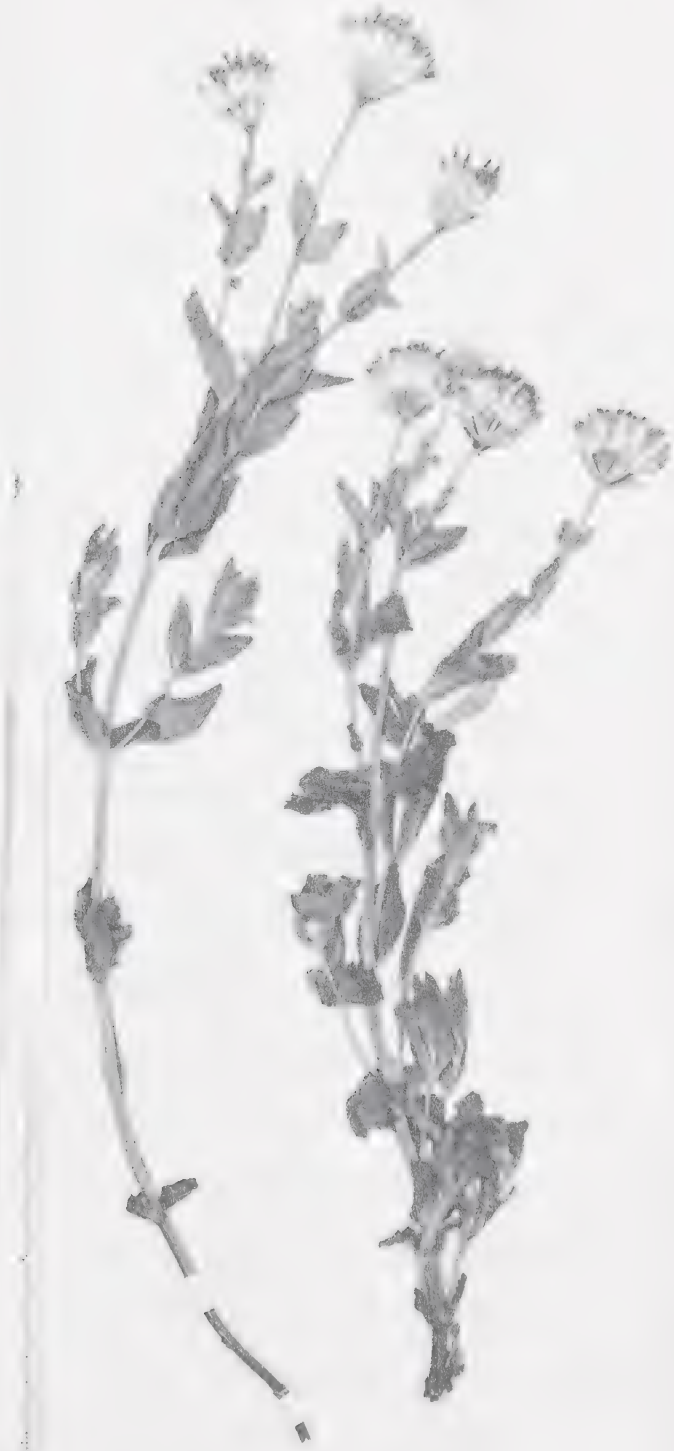
9. Arnica viscosa A. Gray, Proc. Am. Acad. 13:374. 1878. TYPE: Mt. Shasta, California, 8000', Sept. 1877, J.D. Hooker and A. Gray s.n. (Holotype, GH!) (Figure 31).

Raillardella paniculata Greene, Erythea 3:48. 1895. TYPE: near the limit of trees on Mt. Shasta, California, Aug. 4, 1894, W.L. Jepson s.n. (Holotype, NDG!).

Chrysopsis shastensis Jepson, Man. Fl. Pl. Cal. 1037. 1927. TYPE: Horse Camp, Mt. Shasta, California, 8000 ft., W.L. Jepson 59i (Holotype, JEPS!).

Stems usually several branched, prominently ribbed, 20-50 cm high, 3-5 mm diam., strongly stipitate glandular, also becoming densely pilose above; woody caudex 3-5 mm broad, covered with dark scales, lacking basal rosettes; leaves numerous, 5-10 pair on main stem, 2-6 pair on branches, sessile, ovate-oblong to obovate-oblong, (1)2-4(5)cm long, 1-3 cm broad, sparsely to densely pilose and densely stipitate glandular, more or less acute, entire. Inflorescence of 10-20 heads, peduncles 0.5-5 cm long, stipitate glandular and pilose; heads discoid, narrowly turbinate 1-2 cm

Figure 31. Holotype of A. viscosa A. Gray.



[illegible]

HAYDEN'S SURVEY OF U. S. TERRITORIES, 1877 [illegible]

Arnica viscosa [illegible]

SYN. FL. N. AMER.

[illegible] Mt. [illegible]

Cal. [illegible]

high; involucral bracts 10-20, 6-10 mm long, 1-3 mm broad, broadly lanceolate, stipitate glandular and pilose below, acute. Florets 10-30, cream colored, tubular, 6-10 mm long, stipitate glandular; pappus white, rarely tawny, barbellate to subplumose. Achenes dark grey, ribbed, 4.5-6.5 mm long, 1 mm broad, stipitate glandular. Chromosome number 2*n* = 38.

Ecology and Distribution: A very rare species of dry, exposed, pumice slopes at elevations of 1750-2500m. Known localities in Oregon include 3 small populations in Crater Lake National Park, Klamath County and a single collection from the three Sisters area of Deschutes County. Also known from 4 populations in Siskiyou County, California: a large population on Mt. Shasta, 2 populations in the Marble Mountains and a single collection from Preston Peak. An additional population is known from the Trinity Alps, Trinity County, California (Figure 29). Flowers August-September.

Arnica viscosa is one of the rarest and probably the most distinctive species of the genus *Arnica*. This taxon appears to be restricted to volcanic soils and occurs on very open, rocky slopes at high elevations (1750-2500 m) in the Cascades of northern California and southern Oregon. It is known from a few populations in Crater Lake National Park, Oregon; Mt. Shasta, the Trinity Alps, Marble Mountains and Preston Peak, California. An additional population was once collected in the Three Sisters Area of the central Oregon Cascades (*G. van Vechten 219* OSC, GH) however,

repeated attempts by several workers, including myself, have failed to relocate this population.

Arnica viscosa is quite distinctive and easily recognized by its woody caudex; leafy, branching habit; small, sessile, entire leaves; and narrow heads with cream colored florets. In addition, virtually all parts of the plant are densely covered with long glandular hairs so much so that it feels slimy to the touch. Additionally, it has a very distinctive odor which is retained almost indefinitely on herbarium sheets. Virtually all known collections of A. viscosa have been examined and this taxon appears to exhibit virtually no variability from population to population. In fact the only atypical specimens examined were from Upper English Lake, Siskiyou Co., California (F. Oettinger 668 HSC, UC). These plants were less viscid and the upper leaves and branches had a tendency to be sub-opposite to alternate.

Much of the underground parts of A. viscosa, including the caudex and root system, are quite woody. This is probably an adaptation to its rocky, relatively, disturbed habitat on very steep slopes. Much of the root system is exposed, probably due to rock movement associated with heavy winter snows and runoff. As previously noted, the woody caudex and leafy habit common to both A. viscosa and A. venosa is probably coincidental and does not indicate any relationship between the two taxa. The narrow heads, sessile leaves and high altitude habitat, as well as certain flavonoid compounds suggest a closer relationship between A. viscosa and A. latifolia.

The present study is the first in which the types of *A. viscosa* and its two synonyms *Raillardella paniculata* and *Chrysopsis shastensis* have been examined. All three are quite typical of *A. viscosa* and were collected on Mt. Shasta, California; probably at Horse Camp. In his original description of *Chrysopsis shastensis* Jepson cited number *51i* as the holotype, however, according to his notes (Robbins, annotation on type sheet) as well as the designation of "Type" on number *59i*, indicates that this specimen is in fact the holotype for this taxon.

CONCLUSIONS

In the present study nine species, with no infraspecific taxa are recognized in *Arnica* subgenus *Austromontana* (Table 1, page 8). No new taxa are proposed; however, several taxa previously recognized by Maguire (1943) are reduced to synonymy under these nine species. In addition, the division of the subgenus into two sections (*Eulatifoliae* and *Eradiatae*) by Maguire (1943) and the erection of a new subgenus (*Calarnica*) to encompass *A. viscosa* and *A. venosa* (Straley, 1980) are considered artificial and are here rejected.

Within the subgenus *Austromontana* only *A. cernua*, *A. viscosa* and to a lesser extent *A. venosa* are morphologically well defined. The remaining six species are highly polymorphic and exhibit a wide range of morphological intergradation. As previously noted (Gustafusson, 1947; Cronquist, 1955) much of this morphological variability is probably due to apomixis and polyploidy. It is therefore not surprising that the three well defined species *A. cernua*, *A. viscosa* and *A. venosa* are the only entirely sexual, diploid species in *Austromontana* (Straley, 1980). Although highly variable, the species of *Austromontana* are readily recognized by a combination of morphological, ecological and chemical characters (Table 18).

With respect to morphology several evolutionary trends within the subgenus *Austromontana* are readily apparent. Solitary, broad,

Table 18. Comparative characters of the nine species of *Arnica* subgn. *Austromontana*.

	A. cordifolia	*A. cernua*	*A. discoidea*	*A. gracilis*	*A. latifolia*	*A. nevadensis*	*A. spathulata*	*A. venosa*	*A. viscosa*
Stem branching	-	-	+-	+	-(+)	-	+-	+-	++
Underground parts	rhizome	rhizome	rhizome	rhizome	rhizome	rhizome	rhizome	woody caudex	woody caudex
Innovations	+	+	+	+	+	+	+	-	-
Leaves: # pair	2-4	2-3	3-7	2-3	2-4	2-3	3-5	6-10	numerous
shape	cordate	elliptic to ovate	ovate to brd. lanceolate	ovate-lanceolate	ovate	ovate to elliptic	spathulate	ovate to elliptic	ovate-oblong-
margin	dentate	crenate	serrate to dentate	serrate	serrate to dentate	entire	dentate	coarsely serrate	entire
pubescence	±villous ±glandular	glabrous	±pilose glandular	glandular	glabrous	glandular	±villous glandular	±pilose glandular	±pilose glandular
petioles	narrow	narrow	narrow	narrow	sessile	narrow	broad	sessile	sessile
Heads: type	radiate	radiate	discoid	radiate	radiate	radiate	discoid	discoid	discoid
number	1	1	3-10	5-15	3-5	1-3	3-9	1-7	10-20
shape	broadly campanulate	campanulate-turbinate	turbinate-campanulate	turbinate-campanulate	turbinate	campanulate-turbinate	turbinate-campanulate	turbinate-campanulate	narrowly turbinate
Phyllaries: shape	ovate-lanceolate	ovate-lanceolate	ovate-lanceolate	ovate-lanceolate	lanceolate	oblanceolate	broadly lanceolate	ovate-lanceolate	lanceolate
pubescence	pilose ±glandular	±pilose glandular	pilose glandular	glandular	±villous ±glandular	glandular	±villous glandular	pilose glandular	glandular
Pappus: color	white	white	white	white	white	white to tawny	white	white	white (tawny)
setae	barbellate	barbellate to subplumose	barbellate to subplumose	barbellate	barbellate	barbellate to subplumose	barbellate	barbellate	barbellate to subplumose
Achenes: color	dark grey	dark grey	dark grey	black	brown	dark grey	black	dark grey	dark grey
glandular hairs	+-	-	+	■	+-	■	+	-	+
duplex hairs	+	+	+	-(+)	-(+)	-	-	+	-
Chromosome number (2n)	38, 57, 76, 95, 114	38	38, 57, 76	57, 76	38, 76	76	38, 76	38	38
Flavonoids	flavonols simple flavones	flavonols	flavonols simple flavones methylated flavones	flavonols simple flavones highly methylated flavones	flavonols	flavonols methylated flavones	flavonols methylated flavones	flavonols methylated flavones	flavonols highly methylated flavones 6-OH flavones
Habitat	Mesic, montane *Pinus-Abies* forest	serpentine soils, dry, open, low to montane *Pinus* forests	dry Chaparral to montane conifer forests	dry rocky alpine to subalpine *Picea-Abies* forests	mesic to moist montane to subalpine *Picea-Abies* forests	mesic, high-montane *Tsuga-Pinus* forests	serpentine soils, *Pinus-Quercus-Pseudotsuga* forests	hot, dry foothills to low montane *Quercus-Pinus* forests	volcanic soils, dry rocky alpine
Distribution	Yukon to Colorado, Arizona and n California	sw Oregon and nw California	s Washington to s California	Alberta to Colorado, w to Washington and Oregon	Alaska to Colorado and n California	Washington to California	sw Oregon and nw California	Shasta and Trinity Cos., California	c Oregon Cascades to Trinity Co., California

radiate heads with a white, barbellate pappus and relatively broad phyllaries are considered pleisomorphous. In contrast, numerous, narrow, discoid heads with a tawny, subplumose pappus and narrow phyllaries are considered apomorphous. In addition, few, broad, coarsely dentate, long petiolate leaves are considered plesiomorphous while numerous, relatively narrow, entire, sessile leaves are considered apomorphous. Also, a lack of innovations and the replacement of the rhizome by a woody caudex are considered derived features. Additionally, dark grey achenes which lack glandular hairs are considered plesiomorphous while brown and black achenes with glandular hairs are considered apomorphous. *Arnica cordifolia* exhibits virtually every plesiomorphous morphological feature of the subgenus while, in contract, *A. viscosa* exhibits virtually every apomorphous feature.

The basic chromosome number of the subgenus *Austromontana* is $x = 19$. *Arnica cordifolia*, with six chromosome races, is recognized as a mature polyploid complex. Tetraploids ($2n = 76$) are widespread throughout its range, only six widely scattered diploid ($2n = 38$) populations are known, triploids ($2n = 57$) occur mainly in the front ranges of the Rocky Mountains, pentaploids ($2n = 95$) occur in Colorado and two hexaploid ($2n = 114$) populations are known. The triploid race appears to be restricted to disturbed sites, exhibits morphological anomolies and may therefore be a product of hybridization.

Arnica latifolia is largely diploid, however, a significant number of tetraploids have been located in southern Alberta and adjacent Montana and Idaho. Two additional tetraploid populations of this species have been located in the Klamath region. *Arnica gracilis* has both triploid and tetraploid races, suggesting possible introgression and/or polyploidization subsequent to its derivation via hybridization between *A. cordifolia* and *A. latifolia*. *Arnica discoidea*, as well as its derivative *A. spathulata* are largely diploid; however, both contain tetraploid races. *Arnica nevadensis* is wholly tetraploid and the rare endemics *A. cernua*, *A. viscosa* and *A. venosa* are all wholly diploid.

Prior to the present investigation very little was known about the flavonoid chemistry of *Austromontana*. A total of 26 flavonoids, including 12 glycosides and 14 free aglycones, have been isolated and identified in 89 populations of the nine species of *Austromontana*. Several compounds are present in all nine species (e.g., Viscosin and Quercetin Gentiobioside) some are restricted to a few or even only one species (e.g., Apigenin 7-0-glucoside and Luteolin 6OH, 4'methyl ether), certain compounds such as Luteolin 7-0-glucoside and Luteolin 6-Me-7-0-glucoside indicate phylogenetic relationships and the distribution of some compounds (e.g., Quercetin 3-0-glucoside and Kaempferol 3-0-glucoside) appears to be random while other compounds have significant geographical correlations.

An investigation of the flavonoid chemistry of *Austromontana* has proven most useful in deducing new or confirming previously proposed evolutionary relationships. The flavonoid profile of *A. gracilis* is essentially a summation of its two presumed parents *A. cordifolia* and *A. latifolia*. The presence of Luteolin 7-0-glucoside and its 6-methyl ether in *A. cordifolia* and *A. discoidea* suggests a close relationship between the two species. Likewise, the presence of Luteolin 6,4'-methyl ether in both *A. discoidea* and its presumed derivative *A. spathulata* confirms this close relationship. The distribution of two compounds, Kaempferol 6-methyl ether 3-0-glucoside and Quercetin 6-methyl ether 3-0-glucoside, suggests a major phylogenetic division within the subgenus. The former is present in *A. cordifolia* and its presumed derivatives, the latter is present in *A. latifolia* and its possible derivative *A. viscosa*, and both compounds are present in *A. gracilis*, a presumed hybrid between *A. cordifolia* and *A. latifolia*.

Additional significant aspects of the flavonoid chemistry of subgenus *Austromontana* include the depletion of flavonoid profiles in such rare species as *A. cernua* and *A. venosa* and a rare diploid population of *A. cordifolia*. A significant feature of the flavonoid profile of *A. cordifolia* is the restriction of Luteolin 7-0-glucoside and its 6-methyl ether to populations north of the maximum limit of Pleistocene glaciation. This suggests a Pleistocene separation of this taxon into at least two major populations, one north of and one south of the continental ice sheets.

The subgenus *Austromontana* elaborates a wide array of flavonoids including flavonol glycosides, flavone glycosides and both simple and complex methylated flavones and a 6 hydroxylated flavone. The flavonoid profiles of *A. cordifolia* and *A. latifolia* are considered the most plesiomorphous of the subgenus while, in contrast, *A. viscosa* with numerous highly methylated flavones and 6 hydroxylation has the most apomorphous profile.

Arnica cordifolia; with its broad heads, cool-montane ecology, very diverse cytology, seemingly ancient flavonoid profile and wide geographical distribution; is almost certainly the ancestral species of the subgenus *Austromontana*. *Arnica latifolia* with a morphology, distribution, ecology and flavonoid profile very similar to *A. cordifolia* is viewed as an early derivative of the latter. The flavonoid profile of *A. gracilis* as well as its somewhat morphological intermediacy between *A. cordifolia* and *A. latifolia* indicates that it is probably a hybrid between these two species. The flavonoid profile of *A. discoidea*, as well as its morphological resemblance to a rayless *A. cordifolia* clearly indicates a derivation from the latter. In addition, morphological, distributional and flavonoid data indicate that the two rare endemics *A. spathulata* and *A. venosa* are derived from *A. discoidea*. Morphological and chemical evidence clearly establishes that *A. cordifolia* has been involved, at least partly, in the evolution of *A. nevadensis*. *Arnica cernua* shares several morphological features with *A. cordifolia* and is viewed as a derivative of the latter.

Arnica viscosa, with its distinctive apomorphous morphology, ecology and flavonoid profile, shares several features with *A. latifolia* and is probably related to the latter.

A synthesis of all data gathered in the present study suggests the following hypothetical history of the subgenus *Austromontana*. As Maguire (1943) suggested, the genus *Arnica* probably arose in northwestern North America and *A. cordifolia* was probably an early derivative of a hypothetical "protoarnica." Prior to the Pleistocene *A. cordifolia* was diploid and probably relatively widespread in western North America. Its migration outward from its center of origin was probably facilitated by the climatic cooling of the Pliocene and relative ease of migration southward along the north-south trending western cordillera. The diploid *A. latifolia*, an early derivative of *A. cordifolia*, evolved in cooler habitats at higher elevations, possibly as a response to the climatic cooling that began at the close of the Tertiary. The increasing aridity on the west coast at the close of the Tertiary probably also facilitated the derivation of *A. discoidea* from *A. cordifolia*. The presence of Luteolin 7-0-glucoside and its 6 methyl ether in Klamath region populations of *A. discoidea* suggests an early derivation of *A. discoidea* from *A. cordifolia* prior to the elimination of these two compounds in the latter.

The onset of the Pleistocene, with its concomitant climatic cooling and lowering of montane zones, probably provided further opportunity for the southward migration of both *A. cordifolia* and

A. latifolia. Populations of *A. cordifolia* in Arizona, southern Utah and Nevada as well as disjunct populations of *A. latifolia* on Saddle Mountain and Onion Peak, Oregon lend support to this theory (Delting, 1954). In addition, it is clear that *A. cordifolia* as well as many other Rocky Mountain species extended much further eastward during the Pleistocene. The eastern disjunct populations of this taxon in the Black Hills and Cypress Hills are undoubtably the result of this eastward migration. In addition, the disjunct populations of *A. cordifolia* in Manitoba, Michigan and Ontario may be the result of long distance dispersal from this Pleistocene extension of the Rocky Mountain flora.

The derivation of *A. gracilis* via hybridization between *A. latifolia* and *A. cordifolia* probably took place during the Pleistocene, prior to the elimination of the diploid level in the latter. The formation of *A. gracilis* was probably facilitated by the sympatric occurrence of its two parents, the climatic fluctuations and concomitant migrations of floras during the Pleistocene and the creation of many newly disturbed habitats. The presence of both triploid and tetraploid races in *A. gracilis* suggests that allopolyploidy and/or introgression may have occurred subsequent to its formation.

Although the derivation of *A. nevadensis* from *A. cordifolia* is virtually certain, it is unclear as to when this divergence took place. Since *A. nevadensis* shares several plesiomorphous features with *A. cordifolia*, is tetraploid and often resembles little more

than a high altitude ecotype of the latter, it may have initially diverged during the Pleistocene as a high altitude microspecies of A. cordifolia that has become established and more widespread via apomictic reproduction.

There is little doubt that the two Klamath region serpentine endemics A. cernua and A. spathulata originated in late Pleistocene or more recent time, via saltation speciation, from more widespread taxa that gradually became adapted to and later restricted to serpentine soils. This hypothesis has been put forth by Raven and Axelrod (1978) to account for the formation of most of the herbaceous serpentine endemics of the Klamath region. The close morphological similarity between A. spathulata and A. discoidea, as well as the presence of Luteolin 6,4'di-methyl ether in the former and only Klamath populations of the latter, clearly indicates A. spathulata has been derived from A. discoidea. Arnica cernua shares several plesiomorphous features with A. cordifolia and is most likely derived from the latter.

The rare endemic A. venosa is probably a very recent derivative of A. discoidea adapted to hot-dry conditions. This species has a depleted A. discoidea flavonoid profile, intergrades morphologically with, and occurs sympatrically with the latter. Arnica venosa probably evolved as a fire ecotype of A. discoidea, either during the hot-dry post-glacial hypsithermic or more recently.

The derivation of A. viscosa is at best uncertain. This species may be the result of catastrophic selection from a more

widespread Pliocene or Pleistocene taxon that became isolated due to volcanism, mountain building or glaciation. Of all extant species of *Arnica*, *A. viscosa* most closely resembles *A. latifolia*. These two species share several apomorphous morphological features and both contain Quercetin 6-methyl ether 3-0-glucoside. It is therefore suggested that *A. latifolia* is most likely ancestral to *A. viscosa*, possibly through some now extinct intermediate taxon

To summarize phylogenetic relationships in the subgenus *Austromontana*, the two widespread species *A. cordifolia* and its early derivative *A. latifolia* are considered ancestral species of the subgenus. *Arnica cordifolia* gave rise to *A. nevadensis*, *A. cernua* and *A. discoidea*; with the latter giving rise to both *A. spathulata* and *A. venosa*. *Arnica latifolia* may have been involved in the derivation of *A. viscosa* and both *A. cordifolia* and *A. latifolia* probably gave rise to *A. gracilis* via hybridization. This proposed phylogeny therefore suggests that previous infrageneric classifications (Maguire, 1943; Straley, 1980) of *Austromontana* are artificial. Clearly the discoid condition has arisen independently at least twice in *Austromontana* (in *A. discoidea* and *A. viscosa*) more than once in the genus *Arnica* (cf. *A. parryi* of subgenus *Chamissonis*) and numerous times in the Compositae in general (Cronquist, 1977). Maguire's (1943) division of *Austromontana* into radiate and discoid sections is therefore rejected. In addition, since *A. venosa* and *A. viscosa* have very different lineages, their placement in a separate subgenus by Straley (1980) is viewed as artificial and is rejected.

The subgenus *Austromontana*, as circumscribed in the present study, consists of nine species with no infrageneric or infraspecific taxa. The species of this subgenus are bound together by a combination of several morphological features (including broad leaves and a white, barbellate pappus) which, when considered separately, may break down, but when taken in combination readily distinguish them from the other subgenera of *Arnica*. In addition, several flavonoid compounds, including Quercetin Gentiobioside, Viscosin and Apigenin 6 methyl ether, indicate a close relationship between the species of *Austromontana*. Although most of the species of the subgenus are highly polymorphic and tend to intergrade into one or more of the other species, they are readily distinguished by a combination of several morphological, ecological and chemical features. Most of the seemingly limitless morphological variability and apparent intergradation between the species of *Austromontana* is probably due to a combination of several factors including: microspecies formation due to apomixis, environmentally induced polymorphisms and, at least in some species, introgression with other species or populations. In the past, attempts to give taxonomic recognition to every nuance of morphological variability in *Austromontana* has resulted in a very large and cumbersome nomenclature which tended to obscure rather than reflect evolutionary relationships. Therefore, in the present conservative treatment of the subgenus *Austromontana*, nine somewhat distinct points on a morphological and evolutionary continuum have been recognized as taxonomic species.

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APPENDIX

REPRESENTATIVE SPECIMENS

A. cernua

U.S.A.:CA: Del Norte Co.: Gasquet-O'Brien Toll Rd., 7.7 mi. N.E. Patrick Creek Rd., D. Breedlove 3178 (CAS). Boundary Hill, near Telephone Point, A. Eastwood s.n. (CAS). Telephone Point, A. Eastwood 148 (US). Humboldt Co.: Hoopa, J. Davy and W. Blasdale 5645 (UC). Hoopa Indian Reservation, H. Chandler 1298 (NY, UC, US). Ruby Creek, Willow Creek Canyon, J. Tracy 7449 (UC). Horse Mt., J. Tracy 15902 (CAS, UC), S.J. Wolf 471 (ALTA). Willow Creek Canyon, J. Tracy 7057 (CAS, UC). Hoopa Mt., J. Tracy 7561 (UC). Siskiyou Co.: 15 mi. n. Happy Camp, G.L. Stebbins 3269 (UC). Baldy Lookout, F. Hoffman 3547 (UC). Klamath River Canyon, ½ mi. below mouth of Scott River, R. Barneby 11513 (CAS). Trinity Co.: w. side Backbone Ridge on trail to Raymond Flat, E. Carter 1116 (CAS). Mt. Bally, S. Kleeberger s.n. (CAS). OR: Coos Co.: Iron Mt., W. Baker 6822 (OSC, UC). Curry Co.: headwaters Chetco River, R.J. Howell and G. True 48823 (CAS). Josephine Co.: base Coast Mts., near Waldo, T. Howell 166 (ORE), T. Howell 1446 (NDG, UC). Eight Dollar Mt., L. Savage s.n. (UC). Little Rock Creek, 2 mi. s.w. O'Brien, L. Constance and R. Rollins 2993 (CAS, MICH, UC, WTU). Cedar Creek, Deer Creek Canyon, L. Delting 4036 (UC).

Siskiyou Mts., near O'Brien, J. Thompson 1027 (CAS, NDG). Kerby, A. Sweetser s.n. (CAS). Babyfoot Lake Trail, S.J. Wolf 464 (ALTA).

A. cordifolia

CAN: ALTA: Mt. Park, *M. Malte and W. Watson 1969* (UC). Jasper, near Icefields, *A. and R. Nelson 4889* (UC). 1.5 mi E Mulhurst *G. Turner 6750* (ALTA, CAN). Crow's Nest Pass, *J. Macoun 22812* (CAN). Lake Louise, *J. Macoun 65503* (CAN). Bow River Pass, *J. Macoun 14762* (CAN). Squaw Mt., *F. Lewis 92130* (CAN). Mt. Norquay, *B. LaSalle 45155* (CAN). Pyramid Mt., *A.E. Porsild and A.J. Breitung 16351* (CAN). Swan Hills, *E.H. Moss 12442* (CAN). Porcupine Hills, *Malte and Watson 603* (CAN). Lake Louise, *Malte and Watson 1014* (CAN). Bertha Lake, *Malte and Watson 378* (CAN). Mt. Park, *Malte and Watson 1995* (CAN). Columbia Ice Fields, *H. Scoggan 16432* (CAN). Mt. Edith Cavel, *J. Macoun 96072* (CAN). Maligne Lake, *S. Brown 1224* (CAN). 3 mi. N Jasper, *J. Macoun 96025* (CAN). Cottonwood Creek, *E.H. Moss 4654* (ALTA, CAN). Pyramid Lake, *J. Macoun 96019* (CAN). Mt. Eisenhower, *A.E. Porsild and A.J. Breitung 15808* (CAN). Mt. Temple, *A.E. Porsild and A.J. Breitung 12721* (CAN). Sunshine Ski Lodge, *A.E. Porsild and A.J. Breitung 13604* (CAN). Mt. Coleman, *A.E. Porsild and A.J. Breitung 16127* (CAN). Medicine Lake, *M. Dumais 2816* (ALTA, CAN). W. of Lost Lake, Waterton National Park, *J. Kuiyt et al 4046* (CAN). Swan Dive Fire Tower, Swan Hills, *M. Dumais 4024* (ALTA, CAN). Cline River, *M. Dumais 2190* (ALTA, CAN). Palisades Mt., *A.E. Porsild 22526* (CAN). Lake Louise, *M. Dudley s.n.* (DAO). Mt. Norquay, *L. Jenkins 1586* (DAO). Sulfur Mt., *W. Scott s.n.* (DAO). Waterton Lakes, *L.*

Carmichael 88 (DAO). N of Coleman, *M. Kruk 26* (DAO). Cypress Hills, Spring Creek, R.S., *A.J. Breitung 5661* (DAO). Porcupine Hills, 2 mi. N. R.S., *W. Dore 20449* (DAO). Saskatoon Mt., *L. Jenkins 738* (DAO). Cypress Hills, Elkwater Lake, *W. McCalla 3692* (ALTA). Mi. 21, Jasper-Banff Hwy, *W. McCalla 4578* (ALTA). Moraine Lake, *G. Turner 3796* (ALTA). Lake Louise, *G. Turner 11517* (ALTA). Mt. Edith Cawell, *G. Turner 4245* (ALTA). Pyramid Lake, *T. Turner 6872* (ALTA). Maligne Lake, *G. Turner 6903* (ALTA). 20 mi. NW Edson, *I. Corns 12108* (ALTA). Ram Mt., *M.G. Dumais 7767* (ALTA). Red Deer River, *M.G. Dumais 6948* (ALTA). Reeson Lake, Cypress Hills, *P. Scott 1289*. Lake George, *G. LaRoi s.n.* (ALTA). Whitecourt Mt., *J.G. Packer s.n.* (ALTA). Saskatoon Mt., *Praire and Heywood 69* (ALTA). Swan Hills, *M.G. Dumais 4024* (ALTA), *E.H. Moss 12442* (ALTA). Surprise Lake, *M.G. Dumais 6212* (ALTA). Whitehorse Creek, *M.G. Dumais 5669* (ALTA). Jarvis Lake, *M.G. Dumais 2420* (ALTA). Brazeau River, 40 mi. N. Nortdegg, *M.G. Dumais 3006* (ALTA). Saddle Hills, N. of Sexxmith, *E.H. Moss 8464* (ALTA). Winfield, *F. Rusconi s.n.* (ALTA). Mercoal, *E. Woollven 23* (ALTA). Mt. Park, *E. Woollven 7* (ALTA). BC: Alaska Hwy, 12 mi NW Dawson Creek, *Calder and Kukkonen 26801* (UC). ½ mi. S Prince George, *J. Calder and D. Saville 12328* (UC). Mt. Carnarvon, *J. Calder and Saville 12116* (UC). Revelstoke, *W. Spreadborough 64984* (NDG). Lake Osoyoos, *J. Macoun 69323* (NDG). Skagit Valley, *J. Macoun 69325* (NDG). Wipsaw Creek, *J. Macoun 69324* (NDG). Sibley, between Midway and Lake Osoyoos, *J. Macoun 69332* (NDG). 5 mi. S Williams

Lake, *T. McCabe* *953* (UC). SW Corner Dease Lake, *T. McCabe* *8726* (UC). 12 mi. E Golden, *T. McCabe* *6300* (UC). Crownest Pass, *T. McCabe* *6463* (UC). 12½ mi W Prince George, *T. McCabe* *6943* (UC). Takla Landing, *T. McCabe* *7835* (UC). Mt. Pope, *T. McCabe* *7430* (UC). Germansen Landing, *T. McCabe* *7664* (UC). Bowron Lake Rd., *T. McCabe* *8853* (UC). Clearwater, *T. McCabe* *2078* (UC). Grizzly Peak, *T. McCabe* *2260* (UC). 15 mi SW Kleena Kleen, *T. McCabe* *583* (UC). 30 mi N. Kamloops, *T. McCabe* *1031* (UC). Atlin, *Setchell and Parks* *s.n.* (UC). Kimberley, *T. McCabe* *6097* (UC). Sinclair Pass, *T. McCabe* *6219* (UC). Fairview Pass, *T. McCabe* *5907* (UC). Arnarchist Mt., *T. McCabe* *5956* (UC). Ainsworth, *T. McCabe* *5992* (UC). 14½ mi E. Cascade, *T. McCabe* *4644* (UC). Atlin, *A. Eastwood* *651* (CAS, UC). Bear Lake, *T. McCabe* *7997* (UC). Atlin Lake, *A. Eastwood* *6467* (UC). Pavilion Mt., *T. McCabe* *213* (UC). 30 mi. E Bella Coola, *T. McCabe* *1508* (UC). Pinantan, *T. McCabe* *2013* (UC). Mt. Begbie, *T. McCabe* *905* (UC). 10 mi. S Barriere, *T. McCabe* *1938* (UC). 2 mi NW Ft. St. James, *T. McCabe* *7435* (UC). Skeena Crossing, *T. McCabe* *7027* (UC). 14 mi. N. Ft. St. James, *T. McCabe* *7554* (UC). Princeton, *A. McCallum* *s.n.* (UC), Mt. Stephen, *I. Condit* *s.n.* (UC). 18 mi. W Needles, *T. McCabe* *638* (UC). Lake Bootahnie, *J. and E. Thompson* *119* (MICH). 2 mi E. Williams Lake, *J. Calder* *et* *al* *16938* (DAO, OSC). E. side Kootenay Lake, *Beamish and Vrugtman* *s.n* (OSC, UBC). Annaham Lake, *G. Bellinger* *32395* (OSC). Cooper Mt., near Princeton, *Taylor and Szczawin* *s.n* (OSC, UBC). Baribaldi Park, *J. Davidson* *s.n.* (UBC). Creston, *E. Hume* *s.n.* (UBC). Smithers, *J. Menzies*

6016 (UBC). Vanderhoof, J. Eastham 11771 (UBC). 10 mi. E Smithers, V. Krajina et al s.n. (UBC). Cathedral Park, Twin Buttes, R. Hainault 7879 (UBC). Lilloet Lake, J. Pindar-Moss and P. Hamlyn 1116 (UBC). Mt. Edziza, Annas and Klinka s.n. (UBC). Dee Lake, F. Clemens s.n. (UBC). Hedley, T. Taylor 2089 (UBC). Nelson, Silver King Mine, J. Eastham s.n. (UBC). 10 mi. E. Summit Pass, H. Raup and D. Correll 10738 (UBC). 49 mi. E. Teslin, H. Raup and D. Correll 11099 (CAN, UBC). Mi. 98, Haines Rd., T. Taylor et al 993 (UBC). Cassier, T. Taylor et al 398 (CAN, UBC). Mi. 81, Haines Rd., T. Taylor et al 1342 (UBC), Ingenika River, Cassias, G. Copley s.n. (UBC). Mt. Defot, NW Dease Lake, J. Teit 99 (UBC). Iglachuz Mts., N. Anahim Lake, R. Taylor et al 5986 (UBC). Mi. 765, Alaksa Hwy, J. Calder and J. Gillett 25258 (UBC). Mi. 206, Alaska Hwy., A.E. Porsild 9111 (GH). Mt. Finlayson, Vancouver Island, C. Newcomb 60 (GH). Beathson River, H. Raup and D. Correll 10052 (GH). Atlin, J. Bostock 26 (CAN). Tagish Lake, R. Gordon 19 (CAN). Laird Hot Springs, A.E. Porsild and A.J. Breitung 22259 (CAN). Blueberry, A.E. Porsild 8969 (CAN). Coal River, A.E. Porsild 9111 (CAN). Revelstoke, J. Macoun 64984 (CAN). Skagit River, J. Macoun 69324 (CAN). Mt. Brilliant, H. Laing 687 (CAN). Hazelton, J. Macoun 96026 (CAN). Trail, J. Macoun 64981 (CAN). Osoyoos Lake, J. Macoun 69323 (CAN). Telegraph Creek, Dawson s.n. 14731 (CAN). Manning Provincial Park, H. Scoggan 15130 (CAN). Smithers, H. Groh 530 (DAO). 4 mi. N Lower Post, G. Corcoran 58 (DAO). Victoria, J. Tolmie 1053 (DAO).

Cathedral Park, Glacier Lake, R. Hainault 7572 (DAO). Mt. Pope, J. Whitehorn 382 (DAO). Pilot Mt., A. Auclair and S. Eis s.n. (DAO). Blanchard River, 66 mi. S Haines Jct., Calder and Kukkonen 28185 (DAO). Fairy Lake, Calder and Kukkonen 27338 (DAO). Mi. 625 Alaska Hwy, Calder and Gillet 25623 (DAO). Moosehorn Lake, R. Pilfrey 55 (DAO). Mi. 270, Calder and Gillet 25403 (DAO). Hurricane Creek, Atlin Dist., J. Aitken 10 (DAO). 12 mi. N Dawson Creek, Calder and Kukkonen 26801 (DAO). Kootney Nat. Park, Sinclair Nature Trail, K. Seel 27 (DAO). Mi. 32, Atlin Rd., Calder and Gillett 25187. 12 mi. E. Field, G. Turner 3899. 5 mi. WSW Kamloops, Calder and Saville 8492 (DAO). 3½ mi ENE Ft. Steele, R. Taylor and D. Ferguson 619 (DAO). 8 mi. NE Ft. Steele, R. Taylor and D. Ferguson 629 (DAO). 32 mi. W Prince George, Mulligan and Woodbury 1688 (DAO). Manson Creek Village, Calder and Saville 13633 (DAO). W. side Ikanogan Lake, Calder and Saville 8152 (DAO). Kleena Kleen P.O., Calder and Parmelee 19185 (DAO). Pinkut Lake, Calder and Saville 12739 (DAO). 31 mi on rd from Anahim to Bella Coola, Calder and Parmelee 17311 (DAO). Red Rose Mine, Calder and Saville 13380 (DAO). 5 mi. N. Little Fort, Calder and Saville 8638 (DAO). Nuttbide Lake, Guiquet and Ritcey 57 (DAO). 2 mi N. Golden, V. Krajina (DAO). 9 mi. E. Williams Lake, Calder and Parmelee 17040 (DAO). 18½ mi. N. Grand Forks, Calder and Spices 33029 (DAO). MAN: Passburn Tower Cabin, Riding Mt. Provincial Park, A. Lovaas 61-8 (DAO). N.W.T.: Laird River between Nahanni Butte and Simpson, C. Crickmay 114 (CAN). SW MacKenzie Mt., Laird

Range, 15 mi. NW Ft. Laird, W. Jeffrey 424 (CAN). ONT: Ravine Lake, Sibley Provincial Park, C. Garton 15485 (CAN, MICH, UC); 15163 (UC), 15164 (CAN). SASK: Mt. Cabin, Pasquia Hills, J. Rowe 983 (CAN). Cypress Hills: C. Frankton 266 (DAO); R. Newsome 394-64 and 470-64 (DAO); Ledingham and Hudson 1788 (DAO); G. Selleck 394 (DAO); R. Russell s.n. (DAO). YT: Mi. 802, Alaska Hwy., D. Bolinger s.n. (OSC). Mi. 860, Alaksa Hwy., D. Bolinger s.n. (OSC). Whitehorse, J. Gillett and D. Mitchell 3862 (DAO, OSC). Mi. 23, Campbell Hwy., V. Harms 17193 (DAO, GH). Johnsons Crossing, M. Porsild 415 (CAN). Mi. 116, Canol Rd., A.E. Porsild and A.J. Breitung 10079 (CAN). Tagish Lake, A. Pearson 90 (CAN). Alsek River Valley, St. Elias Mt., A. Pearson 67-210A (CAN). Mackintosh, Scofield and Crum 7705 (CAN). Keno, G. Potack 119369 (CAN). Canol Rd., Mi. 95, A.E. Porsild and A.J. Breitung 10527 (CAN), Mt. Sheldon, A.E. Porsild and A.J. Breitung 11103 (CAN). Canol Rd., km. 15.5, S.J. Wolf 507 (ALTA); km. 118, S.J. Wolf 508 (ALTA). 3 mi. S Whitehorse, J. Gillett 3259 (DAO, RM). Mt. Caribou, Gillett and Mitchell 4560 (DAO). Mi. 643, Alaska Hwy., D. Reid 52 (DAO). Lower Kathleen Lake, Kluane Nat. Park, G. and G. Douglas 5884 (DAO). Sockeye Lake, Kluane Nat. Park, G. and G. Douglas 5593 (DAO). Smart River, Cassian Mt., W. Poole s.n. (DAO). Mi. 858, Alaska Hwy, Calder and Gillet 25734 (DAO). Mi. 777, Alaska Hwy, Calder and Kukkonen 28318 (DAO). Mush Creek, Kluane Nat. Park, G. and G. Douglas 9050 (DAO). 16 mi. S. Haines Jct., S.J. Wolf 300 (ALTA). km. 196, Haines Rd., S.J. Wolf 301 (ALTA).

Mi. 110, Haines Rd., S.J. Wolf 302 (ALTA). Mi. 97.8 Haines Rd., S.J. Wolf 303 (ALTA). Mi. 82.5 Haines Rd., S.J. Wolf 304 (ALTA). Km. 1479, Alaska Hwy, S.J. Wolf 307 (ALTA). Alaska Hwy., 1.6 km E Squanga Lake, S.J. Wolf 505 (ALTA). U.S.A.: AK: Sitka, A. Paska s.n. (UC). Mi. 17.5 Haines Hwy. M. Williams 1473 (OSC). Sitka, A. Heller 14942 (WTU). AZ: Apache Co.: Luhachukai Mts., Goodman and Payson 2865 (GH). Rd. to Wide Lake, Lukachukai Mts., C. Mason et al 2441 (UC). Coconino Co.: N. Rim, Grand Canyon, U.S. Park Service 2007 (US). Indian Hollow, Kaibab Plateau, L. Gooding 203 (UC). N. slope, San Francisco Peaks, J. Leiberg 5876 (US). CA: Alpine Co.: Hermit Valley, F. Peirson 11593 (UC). CA: El Dorado Co.: Maggies Peak, H.M. Hall 8810 (UC). Glenn Co.: Black Butte, V. Rattan s.n. (CAS). Humboldt Co.: Salmon Summit, J. Tracy 14372 (UC). Buck Mt., J. Tracy 4177 (UC, WTU). Lassen Co.: 1 mi. E Fredonyer Pass, A. Heller (UC). Milford, T. Brandegee s.n. (UC). Madera Co.: Shadow Lake Trail, 1 mi. fm. Agnew Meadow, J. and C. Reveal 427 (RM, UC, WTU). Mariposa Co.: Yosemite Valley, G. Grant 4356 (UC). Yosemite Cliffs, J. Congdon 247 (UC). Union Pt., Yosemite, J. Congdon s.n. (UC). Yosemite Park, Starden Lake, A. Eastwood 254 (OSC). Signal Peak, C. Quick 1997 (CAS). Modoc Co.: 15 mi. NE Alturas, C.L. Hitchcock (UC). Cedar Pass, J. Weiler 61235 (UC). Happy Camp, L. Whitney 1608 (UC). Mt. Bidwell, M. Manning 250 (UC). Lost Lake, B. Schreiber 1168 (UC). Deep Creek, Alexander and Kellogg 4782 (UC). Emerson Creek, Alexander and Kellogg 4668 (UC). Fandango Pass, I. Wiggens 16457 (CAS). Mono

Co.: Slate Creek Basin, E. Mt. Conness, *J. Clausen 1124* (OSC). Mammoth Lakes, *B. Willard 180* (CAS). Mt. Conness, *C. Mahurin 81* (RM). Mammoth Lakes, Lake Mary, *L. Rose 42194* (WTU). Nevada Co.: Donner Lake, *S.J. Wolf 476* (ALTA). Placer Co.: Deer Park, *H. Geis 38* (UC). W. side Donner Lake, *M. Denton 3901* (WTU). Plumas Co.: Gold Lake Rd., *S.J. Wolf* (ALTA). 1.25 mi. NE Beckwith Butte, *E. Sawyer 27* (UC). American Valley, *R. Austin s.n.* (NDG). Sierraville, *E. Sawyer 116* (UC). Santa Clara Co.: Mt. Hamilton, *R. Pendleton 873* (UC); *M. French s.n.* (UC); *A. Heller 8612* (UC). 2 mi. NNE Mt. Isabel, *C. Graham 412* (UC). Siskiyou Co.: Caribou Lake, *I. Wiggens 13562* (UC). 1.5 mi W. Mt. Shasta City, *E.B. Babcock and G.L. Stebbins 1998* (UC). English Lake, *F. Oettinger 1023* (UC). Abbott's Lake, *F. Oettinger 647* (UC). Marble Mt., *H. Chandler 1615* (UC). Oro Fino, *G. Butler s.n.* (UC). Mt. Shasta, *H. Brown 364* (CAS, UC). Salmon Mts., 10 mi. SW Etna, *A. Eastwood and J. Howell 5037* (CAS). Trinity Co.: Oregon Gulch Mt., *J. Tracy 7538* (UC). Musser Hill, *H. Yates 395* (UC). Grizzly Creek, *E. Carter 996* (CAS). Tuolumne Co.: Gaylor Lakes, *H. Mason 11368* (UC). Dana Fork, *H. Mason 718* (UC). CO: Boulder Co.: Mts. between Sunshine and Ward, *F. Tweedy 4893* (RM). Boulder, *F. Ramaley 71* (RM). Chaffee Co.: Morass Creek, *I. Clokey 3474* (UC). Monarch Pass, *C. Erlanson 2060* (MICH). 15 mi. W Buena Vita, *A. Beetle 2116* (CAS, RM). Clear Creek Co.: Chicago Creek, *J. Ehlers 8402* (MICH). Custer Co.: Westcliffe, *C. Erlanson 1768* (MICH). Douglas Co.: 7.3 mi SW Sedalia, *W. Weber 7440* (WTU). Eagle Co.:

2 mi E Tennessee Pass, I. Tidstrom 4098 (US). El Paso Co.: 2 mi W Palmer Lake, G. Robbins 463 (DAO). Fremont Co.: Sierra Sangre de Cristo, T. Brandegee 241 (UC). Lake Creek, San Isabel N.F., E. Erlanson 1493 (MICH). Gilpin Co.: Tolland, E. Palmer 31255 (GH). Eldorado to Baltimore, F. Tweedy 5823 (RM). Fontleroy Place, H. Rodeck 58 (DAO). Grand Co.: Berthoud Pass, J. Ehlers 8452 (MICH). Sulphur Springs, G. Osterhout 3545 (RM). Berthoud Pass, F. Tweedy 5821 (RM). Gunnison Co.: Bonton Mine, I. Clokey 3009 (UC). Spring Creek Pass, D. Dunn 14707 (OSC). Hinsdale Co.: W Slumgullion Pass, J. Barrell 249-65 (US). Huerfano Co.: Mt. SW Blue Lake, Mosquin and Gillett s.n. (UC). 3 mi below Blue Lakes Camp, R. Rollins 1277 (NDG). Jefferson Co.: Lookout Mt., H. Shacklette 5934 (MICH). Lake Co.: Lost Man Camp, 6 mi W. Independence Pass, U. Waterfall 11623 (UC). Mt. Elbert, I. Clokey 3465 (UC). Lake Creek, I. Clokey 3449 (UC). Everett, I. Clokey 3437 (CAS, RM, UC, US). Leadville, J. Ehlers 8218 (MICH). La Plata Co.: Eagle Pass, Mosquin and Gillett 5430 (UC). Larimer Co.: Rocky Mt. Nat. Park, D. McNeal 202 (RM). Chambers Lake, G. Osterhout 3666 (RM). Mesa Co.: Grand Mesa, U. Waterfall 11653 (UC). Mineral Co.: Wolf Creek Pass, C. Wolf 3007 (CAS). Ouray Co.: Ouray, Biltmore 1149 (US). 2 m W Ouray, Mosquin and Mulligan 5072 (DAO). Pitkin Co.: West Springs Creek, J. Langenhein 1399 (UC). Saguache Co.: Marshall Pass, J. Barrell 29-66 (US). 2 mi N Los Pinos Pass, J. Barrell 161-62 (US). Summit Co.: Breckenridge, K. Mackenzie 80 (RM). 3 mi S. Breckenridge, R. Ferris 11460 (CAS). Breckenridge,

T. Brandegee 241 (UC). ID: Bannock Co.: 3 mi above Pocatello, A. Cronquist 2302 (GH). City Creek, R. Davis s.n. (RM). Bear Lake Co.: Aspen Range, Georgetown Canyon, N. Holmgrem and B. Bethers 4411 (UC). Benewah Co.: SE Plummer, W. Baker 16085 (WTU). Bonneville Co.: Tie Canyon, 6 mi SW Victor, N. Holmgren and V. Marttala 5376 (UC). Butte Co.: Craters of the Moon Nat. Monument, Dole 49 (UC). Camas Co.: Soldier Mts., Ketchum-Featherville Rd., C.L. Hitchcock and C.V. Muhlick 10417 (WTU). Custer Co.: 10 mi W. Cape Horn, C.L. Hitchcock and C.V. Muhlick 9654 (UC). Sunbeam, C.L. Hitchcock and C.V. Muhlick 9008 (UC). Stanley Lake, J. Thompson 13990 (MICH, UC). Stanley Basin, W. Baker 10902 (OSC). Elmore Co.: 23 mi NE Mountain Home, Davidse and Collotzi 453 (UC). Bald Mt., C.L. Hitchcock and C.V. Muhlick 10220 (UC). 4 mi. N. Pine, C.L. Hitchcock and C.V. Muhlick 8750 (UC, WTU). Franklin Co.: 2 mi. SW Franklin Basin R.S., B. Maguire 21645 (WTU). 28 mi NE Preston, R. Bright 60-126 (RM). 31 mi N. Preston, W. Baker 9540 (OSC). Idaho Co.: Warren Summit, R. Davis 2555 (UC). Kinney Point, A. Holmgren and S. Tillett 9607 (UC). 7 Devils Mt., L. Constance 1849 (UC). Kootenai Co.: Albany Falls, C. Speilberg 452 (RM). Latah Co.: Moscow Mt., L. Abrams 613 (UC); L. Constance and R. Rollins 1063 (RM, UC). 1 mi. S Troy, C.L. Hitchcock and C.V. Muhlick 8388 (UC, WTU). 5 mi SE Moscow Mt., W. Baker 8882 (OSC). Lemhi Co.: Moccasin Creek, C.L. Hitchcock and C.V. Muhlick 14287 (UC). 12 mi SW Leadore, C.L. Hitchcock and C.V. Muhlick 8750 (UC). Nez Perces Co.: Laka Waha, A. and E. Heller 3170 (UC). 16 mi E

Spalding, L. Constance et al 1883 (UC). Owyee Co.: Silver City, J. Macbride 955 (RM). 3 mi S. Silver City, W. Baker 8275 (OSC). Rich Co.: Bear Lake Summit, S.J. Wolf 485 (ALTA). Shoshone Co.: Bullion Pass, St. Line, W. Baker 13446 (OSC). Valley Co.: McCall, W. Boone 29 (RM). 3 mi N. Payette Lake, C.L. Hitchcock and C.V. Muhlick 13973 (WTU). 15 mi N. Banks, C.L. Hitchcock and C.V. Muhlick 8578 (WTU). Washington Co.: Mann Creek, H. Tucker s.n. (RM). MI: Keweenaw Co.: 3 mi E. Agate Harbor, F. Hermann 7995 (UC). Fort Wilkins State Park, M. Feigley and L. Nagel s.n. (MICH). Copper Harbor, C. Richards 4675 (MICH). Copper Harbor Cemetery, C. Richards 3783 (MICH); 2221 (MICH). Grand Marias Harbor, C. Richards 2144 (DAO, MICH). 1 mi W Copper Harbor, F. Herman 7761 (MICH, RM). Bluffs SE of Eagle Harbor, M. Fernald and A. Pease 3580 (GH, MICH). Copper Harbor, Pease and Ogden 25178 (GH). MT: Deerlodge Co.: Storm Mt., S.J. Wolf 435 (ALTA). Flathead Co.: 8 km E Bigfork, S.J. Wolf 496 (ALTA). Gallatin Co.: Targhee Pass, S.J. Wolf 433 (ALTA). Middle Creek Canyon, D. Swingle s.n. (MICH). Sage Creek, D. Swingle s.n. (MICH). Glacier Co.: 1 mi N. Logan Pass, G. Rossback 1379 (UC). Lake Co.: Near Biological Station, Flathead Lake, P. Smith 37 (NDG). Lewis and Clark Co.: 8 mi W Lincoln, C.L. Hitchcock 17956 (UC). Lincoln Co.: Mt. Marston, S.J. Wolf 343 (ALTA). 25 km S. Eureka, S.J. Wolf 443 (ALTA). Madison Co.: E of Brandon Lakes, C.L. Hitchcock 16960 (UC). Clover Meadows, Madison Range, C.L. Hitchcock 16843 (UC). Meagher Co.: 35 mi NW White Sulphur Springs, C.L. Hitchcock

16225 (UC, WTU). Rimrock Ridge, C.L. Hitchcock and C.V. Muhlick 12253 (UC, RM). Missoula Co.: Blackfoot Valley, H. LaCasse 15 (MICH). Rattlesnake Creek, Clark and Connor 45 (MICH, NDG). Missoula, Nawrodcki and Neff 2 (NDG). Rattlesnake Valley, W. Olson 3 (NDG). Spring Gulch, Olson and Trott 1 (NDG). Patee Canyon, Burdick and Mueller 4 (NDG). 34 km N. Seeley Lake, S.J. Wolf 495 (ALTA). Marshall Ski Area, S.J. Wolf 492 (ALTA). Jack Creek Canyon; near Yellowstone Park, P.A. Rydberg and E. Bessey 5233 (NDG). Ravalli Co.: 32 mi E. Hamilton, G. Hedgcock s.n. (WTU). Saunders Co.: divide between Camas and Perry Basin, F. Barkley 2568 (NDG). Sweetgrass Co.: 1 mi below Rainbow Lakes, C.L. Hitchcock 16506 (UC). NM: Colfax Co.: Baldy Peak, P. Standley 14307 (US). Hermatite Canyon, D. St. John 52 (GH). Rio Arriba Co.: Chama, P. Standley 6713 (US). Brazos Canyon, P. Standley 10917 (US). Pecos River Natonal Forest, Wuisor Creek, P. Standley 4255 (US). San Juan Mts., 11½ mi NE Chama, R. Bowrman s.n. (UC). NV: Elko Co.: Jarbridge Mts., Coon Creek, P. Train 671 (NDG). Lamoille Lake, A. Holmgren 14177 (UC). Jarbridge Mts., P. Train 618 (UC). Steele Creek, Ruby Mts., A. Borell s.n. (UC). 8 mi W. North Fork, N. Nichols 321 (DAO). Humboldt Co.: Santa Rosa Range, J. Gentry 1581 (DAO, NY RM). Washoe Co.: Headwaters Galena Creek, W. Archer 6677 (DAO, UC). Hunters Creek Rd., 9-11 mi SW Reno, W. Archer 6295 (CAS). White Pine Co.: Wheeler Peak, B. Maguire 21111 (GH, UC); S.J. Wolf 480 (ALTA). OR: Baker Co.: Eagle Creek, T. Gustafson s.n. (UC). East Eagle Trail, G. Mason 5909 (OSC). 6 mi

W Haines, M. Peck 2792 (OSC). Crook Co.: Ochoco N.F., S. Warg s.n. (OSC). Canyon Creek, R. Bratz 16 (OSC). 23 mi NE Primeville, F. Chisaki 780 (RM). Curry Co.: Summit of Pistol River Mt., J. Thompson 4565 (CAS). Waters Creek, 3 mi N Agness, W. Baker 5317 (UC). Deschutes Co.: Pavlina Lake, M. Peck 9658 (OSC). Grant Co.: Malheur N.F., Fields Park, A. Kruckeberg 546 (UC). near Seneca, D. Gren s.n. (OSC). Harney Co.: Myrtle Creek Canyon, M. Peck 2846 (OSC). 15 mi N. Burns, M. Peck 29382 (OSC). Steens Mts., C. Hansen 699 (OSC); 427 (OSC). Fish Lake, W. Lawrence s.n. (OSC). Hood River Co.: Hood River, T. Howell 477 (OSC); L. Henderson 543 (OSC); K. Whited s.n. (NDG). Jackson Co.: Mt. Ashland, M. Peck 2934 (OSC). Siskiyou, W. Sherwood 605 (OSC). 10 mi S Ashland, M. Peck 24903 (OSC). Jefferson Co.: Black Butte, J. Johnson 470 (OSC). Josephine Co.: 4.6 mi S Hugo, K. Chambers 2916 (OSC). Klamath Co.: Fossil Lake, near Crater Lake, H. Furlong s.n. (UC). Whiskey Creek, Beatty and Delting 7771 (OSC). Cow Horn Peak, D. Meanefee 72 (OSC). Swan Lake Valley, E. Applegate 3601 (OSC). Lake Co.: 2 mi NW Crooked Creek, M. Loveless 77 (UC). 1.7 mi S Rt. 140 on Warner Rd., Strother and Ferlatte 960 (UC). Hart Mt., L. Henderson 15733 (OSC). Morrow Co.: Tupper Guard Station, E. Winn s.n. (OSC). Rock Creek, J. Leiberg 92 (GH, UC). Umatilla Co.: 14 km S Ukaih, S.J. Wolf 451 (ALTA). Union Co.: 40 km E Ukaih, S.J. Wolf 450 (ALTA). 3 mi S La Grande, W. Sherwood 215 (OSC). 5 mi E. Kanela, W. Sherwood 212 (OSC). Eagle Cap, G. Mason 1395 (OSC). Jarboe Creek, P. Standley s.n. (OSC). Wallowa Co.:

Lostine River, 18 mi fm Lostine, *J. Murphy* *89* (UC). Ice Lake, *G. Mason* *9084* (OSC). Wallowa Lake, *G. Mason* *5868* (OSC). Mirrow Lake, *G. Mason* *6577* (OSC). Hurricane Creek, *G. Mason* *5365* (OSC). Lick Creek Rd. *H. Gilkey* *8* (OSC). Wasco Co.: 2 mi W The Dalles, *M. Peck* *2791* (OSC); *E. Susmill* *s.n.* (OSC). Wheller Co.: Fossil, *W. Lawrence* *2988* (OSC). SD: Lawrence Co.: Spearfish Canyon, N Black Hills, *F. Bennett* *941* (CAS). 10 mi NW Deerfield, *P. Johnson* *527* (MICH). Top of Custer Peak, *E. Palmer* *37547* (GH). Mt. Rooseveldt, W. Over 17639 (RM). Whitewood, *H. Hayward* *1207* (RM). UT: Beaver Co.: 23 km E. Beaver, *S.J. Wolf* *482* (ALTA). Tushar Peak, *B. Maguire* *19737* (GH, UC). Cache Co.: Logan Canyon, *B. Maguire* *3881* (RM, UC); *W. Dewey* *25* (UC). Carbon Co.: Willow Springs, 1 mi E Sunnyvale, *S. Blake* *9587* (UC). Duchesne Co.: W Mt. Agassiz, *B. Maguire* *et* *al* *4317* (RM). Blind Stream Canyon, Urintah Mt., *B. Harrison and A. Nisson* *8826* (UC). Ashley Nat. Forest, *S.J. Wolf* *396* (ALTA). Garfield Co.: Mt. Ellen, Henry Mts., *R. McVaugh* *14652* (CAS, MICH). Iron Co.: 3 mi N Cedar Breaks Nat Monument, *C.L. Hitchcock and C.V. Muhlick* *4603* (UC, WTU). Cedar Breaks, *A. Eastwood and J. Howell* *7271* (CAS). 13 mi E Cedar City, *B. Maguire* *19454* (UC). 17.2 km E Cedar City, *S.J. Wolf* *481* (ALTA). Juab Co.: Granite Canyon, *B. Maguire and R. Becraft* *2853* (UC). Indian Farm Creek, Deep Creek Range, *B. Maguire and A. Holmgren* *21952* (UC). Trout Creek, *B. Maguire* *2853* (RM). Piute Co.: Marysvale, *M. Jones* *s.n.* (CAS); *5345* (UC); *5887* (UC). Rich Co.: Bear Lake Summit, *S.J. Wolf* *485* (ALTA). Salt Lake Co.: Big Cottonwood Canyon, *P.*

Rydberg and E. Carlton 6652 (UC). Salt Lake, R. Gourley 8089 (UC). Above Alta, B. Maguire 17368 (UC). Big Cottonwood Canyon, W. Cotton et al 16103 (CAS). City Creek Canyon, Salt Lake City, K. Brizzee 7856 (WTU). San Pete Co.: Skyline Drive, B. Maguire 20033 (WTU); S.J. Wolf 393 (ALTA). Summit Co.: Burntfork Creek, E. Jensen s.n. (UC). S of Island Lake, B. Maguire et al 14609 (UC). Tooele Co.: S Willow Creek, Stansbury Range, B. Maguire 21753 (GH, UC). Utah Co.: Mt. Timpanogos, E. Applegate 8439 (CAS). 9.5 km E Mt. Timpanogos, S.J. Wolf 483 (ALTA). Washington Co.: Forsyth Creek, Pine Valley Mts., P. Munz 16924 (WTU). WA: Asotin Co.: Field Springs Park, S.J. Wolf 446 (ALTA). 6 mi W Anatone, H. St John and R. Palmer 9575 (UC). SW Anatone, W. Baker 6001 (DAO, OSC). Clenan Co.: Tumwater Mt., J. Thompson 6479 (WTU). 8 mi Canyon, S. Leavenworth, C.L. Hitchcock 11399 (WTU). S. Navarre Peak, M. Kelly 14 (OSC, WTU). Lookout Mt., J. Thompson 6479 Wenatchee Lake, W. Dress 4228 (UC). 8 mi Camp, A. Kurckeberg 5416 (UC). Clallam Co.: Boulder Creek, Olympic Nat. Forest, G. Jones 8475 (WTU). Columbia Co.: Wolf Fork, Touchet River, H. St. John et al 6971 (UC). Garfield Co.: Blue Mts., D. Peters 385 (UC). Stentz Spring, Blue Mts., L. Constance and H. Clements 1766 (NDG). 15 mi S Pomeroy, C.L. Hitchcock and C.V. Muhlick 8302 (UC, WTU). Kittitas Co.: Virden, J. Thompson 11582 (UC, WTU). Lookout Mt., J. Thompson 14512 (MICH; NDG). Klickitat Co.: NE Bingen, W. Suksdorf 2760 (UC). Mason Co.: Mt. Elinor, P. Freer 371 (WTU). Okanogan Co.: Salmon Creek, C. Fiker 686 (WTU). 12.5 mi NW Loomis, G. and

G. Douglas 3688 (ALTA, DAO). 13 mi E Twisp, G. and G. Douglas 3475 (ALTA, DAO). 20 mi W. Winthrop, G. and G. Douglas 3514 (ALTA, DAO). Chesaw, H. St. John et al 5210 (UC). Pend Oreille Co.: Calispell, F. Kreager 351 (UC, WTU). Metaline Falls, J. Gims 153 (DAO). Skamania Co.: Hamilton Mt., L. Delting 7066 (UC). Snohomish Co.: Mt. Dickerson, R. Owen s.n. (WTU). Spokane Co.: Mt. Spokane, S.J. Wolf 445 (ALTA). Little Spokane River, near Dartford, M. Milburge 308 (NDG). Stevens Co.: E side Columbia River, 12 mi above mouth of Spokane River, H. Rogers 400 (UC). Onion Creek, Northport, G. Hedgcock s.n. (WTU). Yakima Co.: Mt. Aix, J. Thompson 15016 (WTU). Chinook Pass, J. Thompson 15136 (WTU). Windy Pt., Tieton River, F. Warren 1975 (WTU). Mt. Clemens, 5 mi SW Wenas, C.L. Hitchcock and C.V. Muhlick 22418 (WTU). Bald Mt. Rd., H. Broadbooks 65 (MICH). Bald Mt., H. St. John 7854 (UC). WY: Albany Co.: 7.9 mi W Centennial, S.J. Wolf 424 (ALTA). Woods Creek Canyon, C.L. Porter and M. Porter 9810 (UC). Pole Mt., A. Beetle 4729 (OSC, UC). Woods Creek, L. Goodding 1431 (UC). 7 mi W of U of Wyomong Camp., B. Maguire and A. Nelson 13347 (UC). Centennial, Kauffman and Erlanson 113 (MICH). University Camp, Medicine Bow Mts., A. Nelson 7798 (RM). W of Keystone, G. Freytag 132 (RM). Near Albany, R. Asplend 72-14 (RM). Eagle Rock, M. Aslamy 33 (RM). Wash's Fork, A. Nelson 7798 (RM). Lincoln Gulch, A. Nelson 2623 (RM). Big Horn Co.: 10-15 mi E Kane, L. and R. Williams 3016 (RM). Carbon Co.: South Brush Creek Campground, B. and L. Nelson 451 (RM). Clear cuts 1-4, sec.

23T, 14N, R80W, G. Goodwin s.n. (RM). W slope Snowy Range, A. Beetle 4879 (UC). Crook Co.: 6 mi NE Hulett, M. Ownby 599 (RM, UC, WTU). Fremont Co.: Gannett Creek, F. Jozwik 395 (UC). 1 mi S Pacific Spring, C.L. Porter 4525 (RM). Gannett Glacier, F. Jozwik 395 (RM). Union Pass Hills, A. Nelson 871 (RM). Lincoln Co.: Grover Park, Afton Area, O. Harrison 55 (RM). Little White Creek, 1 mi above Allard Flat, T. and V. Call 404 (RM). Natrona Co.: Casper Mt., R. Tresler 55 (RM). Park Co.: Crazy Woman Creek, Beartooth Mts., L. and R. Williams 3518 (NDG). Saunders Co.: divide between Camas and Perry Basin, F. Barkley 2568 (NDG). Sublette Co.: Green River Lakes, A. Beetle 10534 (NDG). Horseshoe Lake, SE Pinedale, C.L. Porter and B. Miller 6057 (UC). Middle Piney Lake, 25 mi W Big Piney, F. and L. Meyer 2400 (UC). Horseshoe Lake, SE Pinedale, C.L. Porter and B. Miller 6057 (RM). 16 km NE Pinedale, S.J. Wolf 427 (ALTA). Teton Co.: Togowotee Pass, S.J. Wolf 430; 432 (ALTA). Teton N.P., Hidden Falls, S.J. Wolf 429 (ALTA). Jackson Hole, J. and M. Reed 2250 (RM). Signal Mt., J. Reed 2860 (RM). Targhee Pass, J. and M. Reed 2903 (RM). Cascade Trail, Teton N.P., B. Schreiber 1266 (UC). Teton N.P., A. Murie 51 (MICH). Camp Davis, Hoback River, L. Wehaneyer et al 5016 (MICH). Washakie Co.: 3 mi E Tensleep, H. Fisser 784 (RM). Yellowstone National Park: 1 mi SE Fishing Bridge, U. Waterfall 15040 (UC). Yellowstone N.P., W. Setchell s.n. (UC). Mammoth Hot Springs, F. Burglehaus 94 (MICH).

A. discoidea

U.S.A.: CA: Butte Co.: Jonesville, E. Copeland 400 (MICH, UC). Contra Costa Co.: Inner Black Hills, W. of "1970," M. Bowerman 2173 (UC). Meridian Peak, M. Bowerman 849 (UC). Del Norte Co.: Black Butte, A. Eastwood 2137 (CAS). Smith River, above Rock Creek Lodge, W. Cooke s.n. (UC). Glenn Co.: Alder Springs, M. Baker 10872 (UC); A. Heller 72758 (UC); J. Howell 19836 (CAS). Humboldt Co.: Croghan Hole, J. Tracy 19273 (UC). Bee Mt., C. Quick 59-31 (CAS). Hoopa Mt., Davy and Blasdale 5668 (UC). Near Willow Creek, J. Tracy 5170 (UC). Trinity Summit, J. Tracy 14154 (UC); J. Tracy 18182 (UC). Horse Mt. J. Tracy 17833 (UC). Briceland, J. Tracy 6335 (CAS, UC). Hoopa Valley, J. Tracy 3513 (UC). White Thorn Valley, J. Tracy 5001 (UC). Lake Co.: Mt. Hull, H.M. Hall 9564 (UC). Coff Mt., H.M. Hall 9595 (UC). Ukiah, H. Yates 3735 (UC). Elk Mt., H.M. Hall 9587 (UC). 1½ mi. W. Oat Hill Mine, I. Wiggins s.n. (UC). Adam's Springs, R. Hoover 5347 (NDG, UC). Eel River, L. Benson 3726 (NDG). 4 mi. W. Lakeport, R. Jameson s.n. (CAS). Marin Co.: Mt. Tamalpais, A. Heller 8392 (UC); K. Brandegee s.n. (UC); W.L. Jepson s.n. (UC); F. Boiletti s.n. (NDG, UC). Pipeline Trail, J. Howell 944 (CAS). Blithdale Canyon, J. Howell 26621 (CAS). Lagunitas, H.M. Hall 8502 (UC). Mariposa Co.: Cathedral Rocks, C. Sharsmith 2168 (UC). Sherlocks, J. Congdon s.n. (CAS). Yosemite Valley, L. Abrams 4527 (UC); H.M. Hall 8867 (UC). Vernal Falls, H.M. Hall and E.B. Babcock 3443 (UC). Camp Curry, H.M. Hall

9078 (UC). Mendocino Co.: 5 mi. E. Point Arena, *L. Rose* *39170* (UC). Point Arena, *A. Eastwood and J. Howell* *6252* (CAS). Rd. between Orrs and Comptche, *A. Eastwood* *11392* (UC). Comptche, *H. Walker* *342* (UC), s. fork, Eel River, *J. Tracy* *5071* (UC). Modoc Co.: John Henry Hill, *M. Manning* *370* (UC). Monterey Co.: Pacific Grove, *A. Elmer* *4402* (CAS, OSC, UC). Chews Ridge, S. Jonesburg, *L. Snyder* *3774* (UC). Los Burros Creek, 15 mi. S.W. Jolon, *C. Hardham* *7037* (OSC). Big Sur, *Y. Mexia* *s.n.* (CAS, UC). Point Lobos, *Helley* *s.n.* (CAS). Chew's Ridge, *C. Hardham* *6202* (CAS). Hanging Valley, Santa Lucia Mts., *D. Breedlove* *36264* (CAS). Jolon, *C. Hardham* *7037* (WTU). Napa Co.: Howell Mt., *J. Tracy* *2224* (UC). White Sulphur Springs, St. Helena, *H. Chandler* *7579* (UC). Monticello Rd., *C. Sharsmith* *5350* (UC). E. side Mt. St. Helena, *R. Hoover* *5014* (UC). Wooden Valley Grade, *P. Raven* *3069* (CAS). Orange Co.: Santa Ana Mts., 4.8 mi. above Gate on Silverado Canyon Truck Trail, *P. Raven* *17751* (UC). Mojeska Springs, Santa Ana Mts., *W. Pequegnat* *s.n.* (WTU). Plumas Co.: S.E. Quincy, *C. Quick* *41-60* (CAS). Taylorsville, *M. Glemens* *s.n.* (CAS). San Luis Obispo Co.: Ocean View Mine, N. of Cambria, *C.B. Hardman* *6828* (CAS, UCSB). Pine Mt., Santa Lucia Mts., *R. Hoover* *8018* (CAS). San Mateo Co.: Skyline Drive, *D. Demaree* *9150* (NDG). Kings Mt. Rd., *D. Keck* *1775* (CAS, OSC, WTU). Portola State Park, *J. Thomas* *9558* (CAS). Santa Barbara Co.: Mudulee Lookout Trai from Big Pine Rd., *E. Blakley* *6056* (CAS). LaCumbre Peak, *D. Breedlove* *3762* (CAS); *D. Breedlove* *585* (CAS, UCSB); *S.J. Wolf* *514* (ALTA). Trail to Mission Pine

Basin, 1-2 mi. W. Big Pine Lookout, C. Smith 8330 (CAS). Santa Clara Co.: Loma Prieta, W. Price s.n. (UC); P. Covel s.n. (CAS). Mt. Hamilton, R. Pendleton s.n. (UC). Summit Santa Cruz Mts., R. Pendleton s.n. (UC); R. Pendleton 394 (UC). Alma Soda Springs A.A. Heller 7490 (UC). Mt. Hamilton, H. Sharsmith 1051 (UC), 3248 (UC). Santa Cruz Co.: Loma Prieta Pk., H. Mason s.n. (UC). Eagle Rock, R. Ferri 11114 (UC). Felton, B. Schreiber 319 (UC). Boulder Creek, T. Kearny s.n. (CAS). Glenwood, H. Davis s.n. (CAS). Redwood Park, S. Blake 11766 (WTU). Shasta Co.: Castle Rock, H. Ripley and R. Barneby 9646 (CAS). Montgomery Creek, E. Bethel s.n. (CAS). Siskiyou Co.: Mt. Eddy, Copeland s.n. (CAS, MICH, NDG, UC, US). China Creek, S. Fork Salmon River, I. Wiggins 13465 (UC). Rainbow Ridge, 1½ mi. Mt. Shasta City, E.B. Babcock and G.L. Stebbins 1997 (UC). Mt. Shasta, E. Palmer 2455 (UC). Trail between Taylor and Cow Creeks, G. Butler 322 (UC). Castle Lake Rd., J. Congdon s.n. (UC). McCloud, A. Eastwood 1105 (CAS, UC). Canyon Creek, branch of Scott River, A. Alexander and L. Kellogg 5620 (UC). Castle Lake, A. Eastwood 10719 (CAS). Sonoma Co.: Guernewood Park, H.M. Hall s.n. (UC). Dohrman Creek, N.E. Jensen's Ranch, H. Mason 8063 (UC). Road to Youngmans, M. Baker 31678 (UC). Tehama Co.: 1.9 mi. above Whitlock Camp, M. Baker and H. Wagon 12833 (UC). Fish Ridge, F. Hoffman 3531 (UC). Trinity Co.: Morrison Gulch Trail, E. Carter 1094 (CAS). Ripstein Campground, P. Munz s.n. (CAS); E. Balls 13687 (WTU). 1.5 mi. above Peanut on Hwy 36, R. Ferris and L. Lorraine 11693 (UC). Salyer, J. Tracy

8015 (UC). White Rock Ranger Station, N. of Yolla Bolly, A. Alexander and L. Kellogg 5115 (UC). Slate Creek, H. Yates 455 (UC). Coffee Creek Canyon, J.T. Howell 1359 (GH, MICH). Dunsmuir Retreat, H.M. Hall and E.B. Babcock 8537, 8539 (UC). Battle Creek, J.T. Howell 13590 (CAS). Tuolumne Co.: Dodge Ridge, Pine Crest, F. Hoffman 1764 (UC). Ventura Co.: Ocean View Trail, near Divide Peak, Santa Ynez Mts., H. Pollard s.n. (CAS). NV: Washoe Co.: Hunter Creek, P. Kennedy 1869 (US). OR: Curry Co.: Iron Mt., W. Baker 5677 (UC). 3 mi. N.E. Brookings, M. Peck 2803 (OSC). Head of Lawson Creek, J. Leach 2250 (ORE). Hood River Co.: Base of Mt. Hood, F. Lloyd s.n. (NY). Bald Butte, M. Armstrong 471 (NY). Hood River, L.F. Hendersn 452 (NY). Mt. Defiance Trail, Columbia Gorge, L. Delting 7169 (CAS, ORE). Hood River, H. Jackson s.n. (CAS). Mt. Hood, near Tollgate, Drake and Dickson s.n. (WTU). Jackson Co.: Ashland, M. Peck 2795 (OSC); 2935 (OSC). Josephine Co.: Noname Creek, S.W. of the Caves, E. Applegate 11917 (CAS). Siskiyou National Forest, 5 mi. E. Jct. 3941 and 3942, M. Denton 2550 (WTU). Klamath Co.: Crater Lake, A. Coonebe s.n. (CAS). E. of Lake of the Woods, E. Applegate 3799 (CAS). Crater Lake, F. Colville and E. Applegate 332 (US); F. Hummewell 7876 (GH). Wasco Co.: 4 mi. E. Bear Springs, J. Thompson 4935 (CAS, WTU). WA: Klickitat Co.: Falcon Valley, W. Suksdorf 7301 (CAS, NY, UC); 12047 (CAS, NY, UC, WTU); 1617 (GH, NY, UC, US).

A. gracilis

CAN: ALTA: Peyto Lake, *W. Weber* *2445* (GH, UBC, UC). Bertha Lake, *A. Breitung* *16228* (UC). Lake Louise Trail, *Malte and Watson* 164A (UC). Lake Louise, *Butters and Holway* *336* (GH, US). Tonquin Valley, *Beamish and Pindar-Moss* *700151*. Maligne Lake, *S. Brown* *1287* (GH, WTU). Lake Louise, *S. Brown* *703* (GH). Bertha Lake, Gadd *and Nagy* 3573 (CAN). Bow Pass, *A.E. Porsild and A.J. Breitung* *16208* (CAN). Mt. Bertha, *Blais and Nagy* *1555* (CAN), Mt. Temple Ski Lodge *A.E. Porsild and A.J. Breitung* *12722* (CAN). Whitehorse Creek, *M. Dumais* *5248* (ALTA, CAN). Sunshine Ski Lodge, *A.E. Porsild and J. Lid* *19570* (CAN). Mt. Eisenhower, *A.E. Porsild and A.J. Breitung* *15807* (CAN). Goat Mt., *J. Macoun* *96043* (CAN). Sofa Mt., *A.J. Breitung* *17178* (DAO). Chief Mt., *A. Breitung* *15867* (DAO). Sofa Mt., *P. Kuchar* *2730* (ALTA). Bertha Lake, *A.J. Breitung* *16228* (ALTA). Maligne Lake, *H. Raup* *2716* (ALTA). Red Rock Canyon, *E.H. Moss* 374 (ALTA). Moraine Lake, *W. McCalla* *4538* (ALTA). Lake Louise, *W. McCalla* *7151* (ALTA). Mi. 105, Banff-Jasper Hwy., *W. McCalla* *7122* (ALTA). B.C.: Ainsworth, *T. McCabe* *5990* (UC). Kinbasket Lake, *T. McCabe* *6275* (UC). Between Burton and Fauquier *T. McCabe* *6629* (UC). Trail, *J. Macoun* *64977* (ND). Kicking Horse Valley, *S. Brown* *298* (US). Mark Creek Falls, Kimberley, *F. Fedor* *80* (UBC). Mt. Matier, *Pinder-Moss and Schofield* *894* (UBC). Sage Creek Falls, *Bell and Davidson* *359* (UBC). Commerce Mt., *Bell and Davidson* *525* (UBC). Little Diamond Head, Garibaldi

Park, E. Peterson s.n. (UBC). Boulder Creek, F. Fedor 100 (UBC). Vancouver Island, Mt. Arrowsmith, C. Rosendahl 1644 (GH). Mt. Assiniboine, A.E. Porsild 18376 (CAN). Lake Agnes, J. Macoun 14757 (CAN). Mt. Forget-Me-Not, J. Macoun 22829 (CAN). Elk River, S. Elko, J. Eastham 15629 (DAO). Flathead Summit, Bell and Davidson 972 (DAO). Emerald Lake, Yoho Nat. Park, W. McCalla 7032 (ALTA, DAO). Tuktakamin Mt., J. Grant 65-5 (DAO). Vermillion Pass, W. McCalla 2014 (ALTA).

U.S.A.: ID: Clark Co.: West Camas Creek, 10 mi. above Kilgore, A. Cronquist 1385 (ND, NY). Custer Co.: 3.5 mi. s.w. Stanley Lake, Hitchcock and Muhlick 9630 (CAS, UC). 11 mi. N.E. Custer, W. Baker 10790 (OSC). Seafoam, Macbride and Payson 3653 (RM, US). McKay, Nelson and Macbride 1497 (RM). Elmore Co.: 10 mi. W. Atlanta, J. and C. Christ 19463 (OSC). Valley Co.: E. side Big Payette Lake, P. Raven 18517 (CAS). MT: Carbon Co.: Rock Creek, 23 mi. S.W. Red Lodge, A. Cronquist 8102 (CAN, CAS, MICH, NY, OSC, WTU). Gallatin Co.: Spanish Basin, P.A. Rydberg and E. Bessey 5229 (US). Glacier Co.: Glacier Nat'l Park, B.R. and C. Maguire 15350 (UC). Lincoln Co.: Leigh Lake, Cabinet Mts., D. Woodland 882 (CAS). Missoula Co.: Holland Creek, Holland Lake, A. Cronquist (CAS, UC). 5 mi. above Bonner, Hitchcock and Muhlick 11432 (CAS, OSC, UC). Powell Co.: Shaw Creek R.S., Flathead N.F., C.L. Hitchcock 18436 (WTU). Ravalli Co.: 4 mi. W. campground, Selway Bitterroot Wilderness, D. Woodland 395 (CAS). Sweetgrass Co.: 6 mi. E. Box Canyon, Boulder River, C.L. Hitchcock 16439 (UC,

WTU). OR: Wallowa Co.: Hurricane Creek, M. Peck 22631 (UC). Boy Scout Ridge, G. Mason 5981 (ORE, OSC). UT: Summit Co.: 4 mi. N. Hayden Pass, H. Bennett 8431 (CAS). WA: Chelan Co.: Mt. Stuart, A. Kruckeburg 2638 (CAN, UC). Hwy 2, 6 mi. N.W. Leavenworth, W. Dress 4281 (UC). Kittitas Co.: Cle Elum River, J. Thompson 10418 (CAS, CAN, WTU). Okanogan Co.: Angles Pass, J. Thompson (CAS, UC, US, WTU). Pend Oreille Co.: "Z" Canyon, 12 mi. N. Metaline Falls, C.L. Hitchcock 2923 (UC, WTU). Pierce Co.: Mt. Rainier, H. Leschke s.n. (CAS). Whatcom Co.: Mt. Hermann, J. Thompson 5352 (GH). WY: Albany Co.: Medicine Bow Mt., A. and R. Nelson s.n. (RM). Laramie Creek, A. Nelson 7568 (RM). Carbon Co.: Chimneys of Pedro Mts., L. Goodding 108 (RM, UC). Fremont Co.: Gannett Peak, F. Jozwik 404 (RM, UC). Snow Lake, R. Scott 9576 (RM). Johnson Co.: Headwaters of Clear Creek and Grazy Woman River, F. Tweedy 3015 (RM). Park Co.: Olson's Meadow, E. and D. Pearson 172 (RM). Sheridan Co.: Big Horn Mts., J. Williams s.n. (RM), A. Nelson 8501 (RM). Sublette Co.: Fremont Lake, E. and L. Payson 2834 (OSC, RM, UC, US). Canyon above New Fork Lakes, E. and L. Payson 4452 (GH). Horseshoe Lake, S.E. Pinedale, C.L. Porter and B. Miller 6069 (RM).

A. latifolia

CAN: ALTA: Lake Louise, *W. Setchell* *s.n.* (UC); *A.E. Porsild and A.J. Breitung* *15770* (CAN); *E.H. Moss* *2903* (ALTA). Banff-Jasper Hwy, *W.A. Weber* *2490* (UC). Banff, *H. Davis* *s.n.* (ND). Waterton Park, Bertha Lake, *W. Malte and W. Watson* *164A* (UC); *A.J. Breitung* *13977* (ALTA). Mt. Edith Cavell, *T. McCabe* *8355* (UC). Sunshine Meadow, Banff Park, *T. Mosquin* *3476* (UC). Sheep Mt., *J. Macoun* *s.n.* (MICH). Vermillion Pass, *R. Ogilvie* *s.n.* (UBC). Cameron Lake, *E.H. Moss* *3034* (UBC). Castlemont, *M. Malte and W. Watson* *488* (CAN). Mt. Temple, *A.E. Porsild and A.J. Breitung* *13753* (CAN). Sunshine Ski Lodge, *A.E. Porsild and A.J. Breitung* *13389* (CAN). Bow River Pass, *A.E. Porsild and A.J. Breitung* *14929* (CAN). 1 mi. S. Belly River Camp, *W. Blais and J. Nagy* *1874* (CAN). Bertha Mt., *W. Blais and J. Nagy* *1703* (CAN). Tower, Waterton Nat. Park, *W. Blais and J. Nagy* *1639* (CAN). Snowshoe Cabin, Waterton Nat. Park, *G. Armstrong and J. Nagey* *4554* (CAN). Chief Mt. L.O., *G. Armstrong and J. Nagey* *4477* (CAN). Crandell Lake, *G. Armstrong and J. Nagey* *3874* (CAN). Cameron Lake, *G. Armstrong and J. Nagey* *4094* (CAN); *W. McCalla* *6699* (ALTA). Crows Nest Lake, *Dawson* *14756* (CAN). Cameron Lake, *W. Dore* *20672* (DAO). Red Rock Canyon, *F. Sudol* *43* (DAO). Mt. Rowe, *A.J. Breitung* *16979* (DAO). Consolation Lake, *W. McCalla* *4546* (ALTA). Bow Pass, *W. McCalla* *6771* (ALTA). Lake Agness, *W. McCalla* *3730* (ALTA). Bald Hills, *P. Kuchar* *521* (ALTA). Ruby Lake, *P. Kuchar* *3007* (ALTA). Marmot

Mt., W. McCalla 3105 (ALTA). BC: E. end Summit Lake, Calder and Saville 10015 (UC). Mt. Fougner at Bella Coola, Calder and Saville 20373B (UC). 10 mi. N Bull River, R. Taylor and D. Ferguson s.n. (UC). Khutze Inlet, T. McCabe 3480 (UC). Indian Point Lake, T. McCabe s.n. (UC). Harrison Creek, 20 mi. N Takla Landing, T. McCabe (UC), Kokanee Glacier, T. McCabe 4741 (UC). Nine Mile Mt., T. McCabe 8181 (UC). Mt. Revelstoke, T. McCabe 5392 (UC). Apex Mt., R. Bowerman s.n. (UC). Green Mt., near Haylmore, J. and E. Thompson 691 (MICH). Mt. Selwyn, H. Raup and E. Abbe 4164 (CAS). Mt. Revelstoke, J. Soper et al 12451 (CAN, CAS). Emerald Lake, C. Shaw 993 (US). Ft. St. James, Calder and Saville 13720 (DAO, US). Selkirk Mts., above Field, H. Peterson 133 (US). Kokanee, J. Eastham 6001 (UBC). Dam Mt., W. Taylor 5993 (UBC). Grouse Mt., V. Krajina s.n. (UBC). Manning Park, Beamish and Vrugtman 60658 (UBC). 44 mi. NNW Dease Lake, S. MacDonald 511 (CAN, UBC). Camp Garibaldi, J. Davidson s.n. (UBC). 12 mi. NE Smithers, V. Krajina et al s.n. (UBC). Ilgachuz Mts., R. Taylor et al 5517 (UBC). 11 mi. N Meziadin Jct., K. Beamish 730079 (UBC). Goodchap Mt., D. Martin s.n. (UBC). E end Summit Lake, Calder and Saville 10015 (UBC). Gold Fish Lake, A. Szczawinski 174 (UBC). Quesnel Dam, W. Newcombe 441 (UBC). Duckling Creek, Germansen Landing, G. Noel 158 (UBC). Mi. 61, Haines Rd., K. Beamish et al 681852 (UCB). Mt. Semour, V. Krajina 333 (UBC). Beatton River, H.M. Raup and D. Correll 10066 (GH). Mt. Fidelity, J. Soper and G. Given 13238 (CAN). Glacier Nat. Park, E. Haber 1508 (CAN). Mi.

85 Haines Rd., C. Clarke 442 (CAN). White Pass, M. Malte 364 (CAN). Summit Lake, 25 mi. W Creston, I. Bassett 4457 (DAO). Floe Lake, K. Seel 189 (DAO). Tunjony Lake, R. Pilfrey 21 (DAO). Wolverine Range, Calder and Saville 13720 (DAO). Van Winkle, 9 mi. SW Wells, Calder and Saville 14175 (DAO). Yanks Peak, Calder et al 18083 (DAO). Blackwall Peak, Calder and Saville 10587 (DAO). Alpine Mt., 12 mi. NNE Nelson, Calder and Saville 11129 (DAO). Red Rose Mine, Calder and Saville 15190 (DAO). Mt. McLean at Lillooet, Calder and Saville 15505 (DAO). Mt. Burman, Calder and Mackay 32595 (DAO). 75 mi. S Haines Jct., Calder and Kukkonen 28154 (DAO). Murtle Lake, L. and T. Ahti 6784 (DAO). 13 mi. E Terrace, R. Pilfrey 84 (DAO). Lake in Coast Range, 58°41' N, 133° 04'W, R. Pilfrey 79 (DAO). Queen Charlotte Islands: 20 mi. S. Morseby Logging Camp, Calder et al 23046 (CAS, DAO, OSC, UBC, UC). Tasau Sound, Calder and Taylor 23525 (DAO, UBC). McClinton Bay, Calder et al 21637 (DAO). Shields Bay, Calder et al 2331 (DAO). Lake Takakia, Calder and R. Taylor 36296 (DAO). Kootenay Inlet, Calder and R. Taylor 36151 (DAO). Mt. Morsby, Calder and R. Taylor 36440A (DAO). Vancouver Island: Green Mt., V. Krajina et al 5004 (UBC). Mt. Arrowsmith, G. Allen s.n. (UBC). Mt. Bechy, J. Soper et al 12361 (CAN). Shaw Creek, W. Spreadborough 96037 (CAN). Moat Lake, J. Underhill 327 (DAO). Sproat Lake, T. Taylor 1238 (DAO). Crest Lake, A. Young and W. Hubbard 580 (DAO). NWT: 62° 46'N, 129° 1'W, L. Allison 29 (DAO). YT: White Pass, A. Eastwood 936 (UC). Mi. 268, Canol Rd., A.E. Porsild and A.J. Breitung 11374

(CAN, UC, US). Mi. 95, Canol Rd., A.E. *Porsild and A.J. Breitung* *10228* (CAN, GH, UC, US, WTU). Upper Hyland Lake, *Calder and Kukkoun* *27809* (CAS, DAO, GH). Mi. 284-290, Canol Rd., *A.E. Porsild and A.J. Breitung* *11269* (CAN). Canol Rd., NW end of Its Range, *A.E. Porsild and A.J. Breitung* *11394* (CAN). Kluane National Park, Alsek River, *G. and G. Douglas* *8953* (DAO). Kluane National Park, Bates Lake, *H. and I. Weaver* *803* (DAO). Cassiar Mts., *W. Poole* *49* (DAO). Mt. 4 mi. W Upper Hyland Lake, *Calder and Kukkonen* *27909* (DAO). 62° 11'N, 129° 17'W, *L. Allison* *40* (DAO). Goatherd Mt., Kluane National Park, *G. and G. Douglas* *7015* (DAO). U.S.A.: AK: Hatcher Pass, *S.J. Wolf* *503* (ALTA). Craig, *I. Norberg* *s.n.* (UC, US). Hatcher Pass, *J. Langenheim* *4260* (UC). Yakutat Bay, *F. Funston* *79* (CAN, ND); *122* (ND). Olga Bay, Kodiak Island, *S. Blake* *553* (ND); *E. and H. Looff* *490* (ND, UBC). Deer Mt., *F. Went* *80* (UC). Silver Bow Basin, *E. Shumway* *s.n.* (UC). Yes Bay, *T. Howell* *1634* (UC). Sitka, *W. Wright* *1537* (UC). Deer Mt., *T. McCabe* *8635* (UC). Harris Peak, Prince of Wales Island, *D. Jaques* *1569* (OSC). Indian River, Sitka, *L. Smith* *s.n.* (OSC). Virginia Mt., Prince of Wales Island, *D. Jaques* *1440* (OSC). Duchess Mine, Latouche Island, *H. Shacklette* *4704* (MICH). Cairn Ridge, near Juneau, *H. Shacklette* (MICH). Curry Lookout, *L. Jordal* *2555* (MICH). Hatcher Pass, *M. Williams* *1206* (OSC). S fork Campbell Creek, near Anchorage, *M. Williams* *1841* (OSC). Mt. Roberts, Juneau, *M. Williams* *1392* (OSC). Kenai Lake, *J. Calder* *6089* (CAS, DAO). Kuiu Island, *E. Walker* *774* (CAS, US). 3 St's.

Bay, Kodiak Island, W. Eyerdam 602 (CAS, US). Katalla, 50 mi SE Cordova, S. Tathill B116 (CAS). Eyak Lake, Cordova, M. Hanna s.n. (CAS). Skagway, A. Eastwood 818 (CAS, US). Sitka, G. Haley s.n. (CAS). Karluk, Kodiak Island, C. Rutter 159 (US). Haines, E. Scheuber s.n. (US). Sitka, C. Piper 4245 (US). Windham Bay, J. Culberson 4956 (US). Stikine Glacier, W. Cooper 72 (US). Peters Creek, R. Scott s.n. (UBC). Mt. Marathon, J. Calder 5899 (UBC). Juneau, E. Scamman 1123 (GH). Mt. Roberts, A. and R. Nelson 4440 (GH). Mt. Crillion, R. Bates 160 (GH). Barren Island, I. Gabrielson s.n. (GH). Kenai Lake, J. Beaman 652 (CAN, GH). Alaska Range, 62° 40'N, 152° 30'W, L. Viereck 5259 (CAN). Burron Bay, H. Canavan 5683 (CAN). Ketchican, J. Anderson 2A691 (CAN). Orca, I. Norberg s.n. (CAN). Burma Rd., Mi. 74, Richardson Hwy., L. Spetzman 3319 (CAN). Willow Rd., Fern Mine, G. Frohne 49-359 (RM). Mt. Marathon, J. Calder 6642 (DAO). Palmer Creek Valley, SE Hope, J. Calder 6233A (DAO). Chugach Mts., Anchorage, Dutilly et al 21143 (DAO). CA: El Dorado Co.: S side Echo Lake, A. Heller 12544 (UC). Sugar Bowl Mt., L. Kildale s.n. (UC). Trinity Summit, J. Tracy 17236 (UC); 10736 (UC). Nevada Co.: Donner Pass, A. Heller 7029 (MICH). Trinity Co.: Salmon Mts., Union Creek, H.M. Hall 8648 (UC). Mary Blaine Mt., J. Tracy 14439 (UC). Siskiyou Co.: Jackson Lake, A. Alexander and L. Kellogg 183 (UC). Bolan Lake, C.L. Hitchcock and J. Martin 5233 (UC); S.J. Wolf 465 (ALTA). Marble Mt., H. Chandler 1699 (UC). Hancock Lake Trail, Marble Mt. Wilderness, F. Oettinger 460 (UC). Spirit

Lake, Marble Mts., *J. Howell 14910* (CAS). Caribou Basin, Trinity Alps, *J. Howell 13380* (CAS). Waldo-Happy Camp Rd., *F. Hoffman 2607* (DAO). 8.3 mi. from Etna on rd to Sawyer's Bar, *E. Balls 13942* (WTU); *S.J. Wolf 467* (ALTA). CO: Chaffee Co.: Monanos Creek, *I. Clokey 3500* (RM, UC). Clear Creek Co.: Loveland Pass, *S.J. Wolf 416* (ALTA). Gunnison Co.: Queen's Basin, *J. Langenheim 3908* (RM, UC). Ohio Peak, *J. Barrell s.n.* (US). Lake Co.: Lake Creek, *I. Clokey 3515* (UC). Larimer Co.: Rocky Mt. National Park, Rainbow Curve Trail, *U. Waterfall 14958* (UC); Trail Ridge, *E. Smith 40* (UC). Lock Vale, Estes Park, *I. Clokey 3962* (CAN, MICH, UC). Cameron Pass, *G. Osterhout 3795* (RM). Lulu Pass, *G. Osterhout 3876* (RM). Lake Helene Trail, Rocky Mt. National Park, *R. Ashton 70-g-7* (RM). Estes Park, *G. Osterhout 1371* (RM). Routt Co.: Hahn's Peak, *W. Weber 6929* (RM, WTU). ID: Bear Lake Co.: Bloomington Lake, *R. Davis 1613* (UC); *W. Baker 9394* (DAO, OSC). Benewah Co.: Bald Mt., *W. Baker 13388* (OSC). Blaine Co.: 5 mi. from Alturas Lake, *C.L. Hitchcock and C.V. Muhlick 10534* (UC). Norton Peak, *C.L. Hitchcock and C.V. Muhlick 10709* (RM). Boise Co.: Jackson Peak, *C.L. Hitchcock and C.V. Muhlick 10026* (CAN, UC). Bonner Co.: Queen Mt., *W. Eggleston 9770* (US). Bonneville Co.: *E. Payson and G. Armstrong 3511* (RM). Custer Co.: 1 mi E Castle Peak, *C.L. Hitchcock and C.V. Muhlick 10913* (UC). Josephus Lake, *J. McBride and E. Payson 3581* (RM, UC). Mt. Mogg, *C.L. Hitchcock and C.V. Muhlick 11236* (UC, WTU). 3.5 mi SW Stanley Lake, *C.L. Hitchcock and C.V. Muhlick 9630* (CAN). Yankee Fork, *C.L. Hitchcock and*

C.V. Muhlick 9569 (WTU). 10 mi S Atlanta, C.L. Hitchcock and C.V. Muhlick 10247 (RM, UC, WTU). Franklin Co.: 2 mi SW Franklin Basin R.S., B. Maguire 21643 (CAN, UC). Fremont Co.: Ponds Lodge, Targhee N.F., W. Baker 9831 (OSC). Idaho Co.: Lolo Trail, 65 mi E Pierce, C.L. Hitchcock and C.V. Muhlick 21921 (UC). Walde Mt., L. Costance and R. Rollins 1687 (ND). Coolwater Mt., L. Constance and F. Pennell 1985 (UC). Pilot Knob, W. Elwood 36 (UC). Burnt Knob Lookout, W. Baker 12638 (OSC). Salmon Mt., Q. Jones 333 (CAS, WTU). Lemi Co.: 9 km. S Lost Trail Pass, S.J. Wolf 488 (ALTA). S Fork Camas Creek, 40 mi. NW Challis, C.L. Hitchcock and C.V. Muhlick 11330 (UC). Shoshone Co.: St. Maries River, C. Wilson 103 (UC). Freezout Saddle, C. Wilson 286 (UC). 4 mi. E Burke, A. Cronquist 6063 (CAN, UC, US, WTU). 14 mi. E Clarkia, W. Baker 16208 (WTU). Thompson Pass, W. Baker 16208 (WTU). Valley Co.: Lick Creek Summit, S.J. Wolf 357 (ALTA). Gold Fork Lookout, J. Thompson 13745 (MICH, UC). Elk Summit, R. Davis 2658 (UC). Upper Payette Lake, W. Baker 10357 (OSC). MT: Beaverhead Co.: Pintlar Falls, C.L. Hitchcock and C.V. Muhlick 12784 (UC). ¼ mi. below Ajax Mill, C.L. Hitchcock and C.V. Muhlick 12656 (OSC, UC). Torrey Lake, C.L. Hitchcock and C.V. Muhlick 15052 (UC), Pintlar Creek, C.L. Hitchcock and C.V. Muhlick 12758 (RM, UC). Lake Waukena, C.L. Hitchcock and C.V. Muhlick 13105 (OSC); O'Del Lake, C.L. Hitchcock and C.V. Muhlick (WTU). Deerlodge Co.: Storm Lake, C.L. Hitchcock and C.V. Muhlick 14830 (RM). Storm Lake Rd., S.J. Wolf 435 (ALTA). Fergus Co.: Big Snowy Mts., 31 mi SW Lewis-

ton, G. and F. Ownby 2417 (RM, UC). Flathead Co.: Bowman Lake, R. Turley 212 (UC). Gallatin Co.: 8 mi. E Eldridge, C.L. Hitchcock and C.V. Muhlick 15149 (UC). Glacier Co.: Glacier National Park, N. Carlson s.n. (UC); H. and V. Bailey 423 (UC); B. Maguire and G. Piranian 15366 (UC); B. Maguire et al 15346 (UC). 16.7 mi NW Kwiua, T. Stuessy 1616 (UC). Granite Co.: Burnt Fork Trail, C.L. Hitchcock and C.V. Muhlick 14502 (WTU). Lake Co.: 10 mi NE Polson, J. Thomas 11051 (CAS). McDonald Lake, C.L. Hitchcock and C.V. Muhlick 18235 (RM). Lewis and Clark Co.: 25 mi. NW Agusta, C.L. Hitchcock 17997 (RM, UC). W slope Trident Peak, C.L. Hitchcock 18748 (UC). Lincoln Co.: Mt. Marston Rd., S.J. Wolf and P. and D. Wolf-Thompson 344 (ALTA). Madison Co.: Upper Brandon Lake, C.L. Hitchcock 17045 (RM). Missoula Co.: 2 mi. E Holland Lake, C.L. Hitchcock 18357 (UC, WTU). 10 mi. W Placid Lake, C.L. Hitchcock 18165 (RM, UC). 1 mi. W Gordon Pass, C.L. Hitchcock 18402 (UC). Park Co.: 5 mi. E Cooke City, J. Witt 1755 (WTU). Powell Co.: 3 mi. W Big Salmon Lake, C.L. Hitchcock 17162 (WTU). Ravalli Co.: St. Mary's Creek, C.L. Hitchcock and C.V. Muhlick (CAN, UC). Stillwater Co.: Mt. Haystack, C.L. Hitchcock and C.V. Muhlick 13429 (CAN, OSC, UC, WTU). Sweetgrass Co.: Crazy Mts., Big Timber Creek, C.L. Hitchcock and C.V. Muhlick 13288 (OSC, UC). 1 mi. S Rainbow Lakes, C.L. Hitchcock and C.V. Muhlick 16507 (CAN). OR: Clackamas Co.: SW slope Mt. Hood, H. and J. Thomas 248 (UC). Clatsop Co.: Saddle Mt., S.J. Wolf 379 (ALT); J. Davis s.n. (OSC); G. and R. Rossbach 377 (CAS). Onion Peak, L. Heckard

1606 (UC); K. Chambers 3149 (CAS, OSC, WTU); L. Heckard 1623 (OSC). Sugarloaf Mt., K. Chambers 3764 (OSC, WTU). Curry Co.: Iron Mt., S.J. Wolf 457 (ALTA). Above Agness, E. Applegate 7153 (CAS). Summit, Pistol River Mt., J. Thompson 4565 (WTU). Douglas Co.: Black Rock Lookout, D. Overlander s.n. 1944 (OSC). Twin Lakes Mt., 40 mi. E Glide, V. Crosby 336 (OSC). Grant Co.: Strawberry Mt., W. Cusick 3565 (WTU). Harney Co.: Stein's Mt., P. Train s.n. (OSC). Hood River Co.: Mt. Hood, P. Munz 14461 (UC); G. Jones (WTU), H.M. Hall s.n. (UC). Jackson Co.: Mt. Ashland, M. Peck 2934 (OSC); B. Jackson s.n. (CAS). Jefferson Co.: J. Johnson 462 (OSC). Josephine Co.: Big Meadow, SE Oregon Caves, E. Applegate 11243 (UC). Bolan Lake, J. Thompson 12510 (UC, WTU). Mooney Mt. A. Sweetser s.n. (UC). Near Deer Creek, A. Sweetser s.n. (UC). Lake Mt., E. Applegate 11465 (OSC, UC). Sexton Mt., L. Savage s.n. (UC). Bolan Lake, M. Peck 23841 (OSC). 5 mi. SE Oregon Caves, M. Peck 8334 (OSC). Millers Lake, A. Steward 7180 (OSC). Lane Co.: Fairview Mt., L. Constance s.n. (UC). Benson Lake, L. Constance s.n. (UC). Horse Pasture Mt., M. Peck 23841 (OSC). Fairview Lookout, H. Gilkey s.n. (OSC). Fairview Mt., W. Baker 5565 (OSC, WTU). Linn Co.: Breitenbush, M. Peck 18718 (UC). Jefferson Park, L. Leach 14754 (OSC). Mt. Jefferson, M. Peck 9109 (OSC). Monument Peak, A. Aller 812 (OSC). Marion Co.: 1 mi. E Breitenbush, M. Peck 18718 (OSC). House Mt., M. Peck (OSC). Tillamook Burn Area, 3 mi. SE Blue Lake, K. Chambers 4149 (OSC). Union Co.: Anthony Creek, Blue Mts., W. Cusick 3820 (WTU). Wasco Co.: 5 mi.

W Mosier, J. Thompson 4224 (WTU). Bear Springs, Mt. Hood N.F., J. Thompson 5169 (WTU). Washington Co.: Tillamook Burn, N of Wilson River Hwy., K. Chambers 4052 (OSC). UT: Cache Co.: Tony Lake, A. Holmgren and C. Biddulph 8172 (UC). White Pine Lake, B. Maguire et al 14081 (CAN, UC). Mt. Naomi, B. Maguire et al 14154 (GH, UC, US). Trail to Mt. Naomi, B. Maguire 16140 (WTU). Duchesne Co.: Blind Stream Rd., NW Hanna, S.J. Wolf 397 (ALTA). Salt Lake Co.: Big Cottonwood Canyon, W. Cooper 329 (RM); A. Garrett 1509 (RM). Summit Co.: Stillwater Ford, Uintah Mts., E. and L. Payson 4995 (RM). Utah Co.: Mt. Timpanogos, B. Maguire 17507 (UC). 1 mi. E Brighton, B. Maguire 17406 (GH). WA: Chelan Co.: Mt. Stuart, J. Thompson 7685 (CAS, UC). Mt. Ingalls, W. Eyerdam s.n. (UC). Blue Lake, near Washington Pass, G. Ward 136 (WTU). Clackamas Co.: Mt. Hood, J. Thompson 3403 (WTU). Clallam Co.: Hurricane Ridge, W. and M. Muenscher 10004 (UC); G. Jones 3351 (WTU). Mt. Angeles, J. Thompson 7522 (CAS, UC, WTU). Columbia Co.: 1.5 mi E Table Rock, Umatilla N.F., A. Kruckeberg 2514 (UC). Grays Harbor Co.: Colonel Bob L.O., J. Thompson 7245 (WTU). Jefferson Co.: Olympic Mts., Mt. Constance, R. Rollins and T. Chambers 2654 (UC). King Co.: Goldmeyer Hot Springs, J. Broadbent s.n. (WTU). Mt. above Embro, I. Otis 708 (WTU). Kittitas Co.: Mission Peak, J. Thompson 14913 (CAS, MICH, UC, WTU). Scatter Creek Trail, C.L. Hitchcock 8017 (UC); A. Kruckeberg 2966 (OSC, UC). Klickitat Co.: Mts. NE Bingen, W. Suksdorf 2760 (WTU). Mason Co.: Mt. Ellinor, W. Eyerdam 1276 (UC). Pierce Co.: Yakima

Park, Mt. Rainier N.P., B. Maguire 17260 (UC). Paradise Inn, Mt. Rainier N.P., L. Abrams 9047 (UC). Paradise Valley, H. Parks 296 (UC). Mt. Rainier, L. Benson 2337 (UC). Chinook Pass, W. Eyerdam s.n. (UC). Mt. Rainier National Park, B. Maguire 17258 (UC). Cowlitz Pass, J. Thompson 11102 (CAS, WTU). Skamania Co.: Big Lava Beds, J. Franklin 448 (OSC). Mt. St. Helens, F. Coville 747 (US, WTU). Snohomish Co.: Mt. Pugh, J. Thompson 14351 (CAS, MICH, UC). Mt. Dickerman, J. Thompson (WTU). Whatcom Co.: Mt. Baker, W. Muenscher 8030 (UC). Yakima Co.: Chinook Pass, J. Thompson 15136 (CAS, MICH, UC, WTU). Mt. Adams, W. Suksdorf 531 (UC). Mt. Paddo, W. Suksdorf 6369 (UC). Mt. Aix, J. Thompson 15016 (CAS, MICH, UC, WTU). Mt. Adams, J. Langdon and T. Gustafson 138 (UC). WY: Albany Co.: 7.4 mi. W Centennial, S.J. Wolf 422 (ALTA). 7.9 mi. W Centennial, S.J. Wolf 424 (ALTA). Lincoln Co.: Jackson's Hole, E. and L. Payson 2276 (UC). Afton Area, W. Sheep Pass, O. Harrison 54 (RM). Sublette Co.: 26 mi. W Big Pinney, F. and L. Meyer 2369 (UC). Teton Co.: Skyline Trail, Teton N.P., L. Wehmeyer et al 5450 (MICH). 1 mi. E Togwotee Pass, S.J. Wolf (ALTA). Yellowstone National Park: Obsidian Creek, A. and E. Nelson 6108 (UC). Between Old Faithful and West Thumb, B. and R. Maguire 1249 (UC).

A. nevadensis

U.S.A.: CA: Sierra Valley, Lemmon s.n. (UC). Truckee River, above Shingle Mill, C. Sonne s.n. (UC). Open moist woods, middle Tule River, C. Purpus 1540 (UC). Coburn Mill, T. Brandegee s.n. (UC). Middle Tule River, C.A. Purpus 5625 (GH, UC, US). Amador Co.: G. Hansen 416 (UC). ½ mi. S. Kirkwood Lake, G. Robbins 3764 (CAS). Butte Co.: Jonesville, A. Heller 12861 (OSC). El Dorado Co.: Fallen Leaf Lake, G.L. Stebbin 2032 (UC). Angora Peaks, H.M. Hall 8796 (UC). Velma Lakes Trail, above Eagle Lake, G. Robbins 2054 (UC). Red Peak, G. Robbins 1806 (CAS, UC). Fallen Leaf Lake, M. Baker s.n. (UC). Angora Peak, G. Hall s.n. (UC). Fresno Co.: Vidette Meadows, J. Howell 24955 (CAS). Fish Camp, P. Raven 5786 (CAS). Mills Creek, P. Raven 5674 (CAS). Kip Camp, P. Raven 7361 (CAS). Pocket Meadow, P. Raven 6006 (CAS). Glenn Co.: Black Butte, J. Howell 19250 (CAS), W. and I. Knight 2529 (CAS). Inyo Co.: Flower Lake, S. Austin 558 (UC). Big Pine Lakes, J. Howell 23815 (CAS). Box Lake, J. Howell 22445 (CAS). Rock Creek Lake, J. Howell s.n. (CAS). Madera Co.: Garnet Lake, J. Howell 16479 (CAS). Shadow Lake, P. Raven 3390 (CAS). Lake Ediya, P. Raven 3527 (CAS). Mariposa Co.: Yosemite Park: Glacier Point, H.M. Hall 9149 (UC). Fletcher Lake, B. Schreiber 2013 (UC). Donohue Pass, B. Schreiber 1787 (UC). Mt. Dana, H.M. Hall and E.B. Babcock 3599 (UC). Lost Lake, H.M. Hall 9068 (UC). The Fissures, H.M. Hall s.n. (UC). Glacier Point, A. Perkins s.n.

(OSC). Mono Co.: Mt. Lyell, A. Hawbecker s.n. (UC). Tioga Crest, H. Mason 11469 (UC). Mt. Dana, C. Sharsmith 2426 (UC). Harvey Monroe Hall Natural Area, J. Clausen 1124 (UC), P. Stockwell 1346 (CAS). Mt. Dana, Sharsmith 2088 (CAS). Sonora Pass, A. Eastwood and J. Howell 7565 (CAS). Nevada Co.: Stanford Peak, A. Kellogg s.n. (UC). Summit-Soda Springs, Kennedy and Doten 274 (UC). Donner Pass, J. Howell 18662 (CAS). S. side Donner Lake, A. Heller s.n. (CAS). Placer Co.: Mt. Anderson, C. Sonne s.n. (CAS, UC). Truckee River, C. Sonne 7 (GH, UC). Truckee, C. Sonne 27 (GH). Plumas Co.: Gold Lake Road, J. Ewan 8206 (UC). Shasta Co.: Helen Mt., G. Gillett 1078 (CAS). Lassen Peak, R.M. Austin s.n. (GH). Lassen National Park, F. Hermann 11956 (US). Sierra Co.: Gold Lake, H. Baker 82 (CAS). Siskiyou Co.: Taylor Lake, D. Barbe 129 (UC). Medicine Lake, H. Baker 502 (UC). Upper English Lake, F. Oettinger 1082 (UC). Wildcat Peak, Alexander and Kellogg 204 (UC). Marble Mt., H. Chandler 1615 (CAS). Tehama Co.: Brokeoff Mt., G. Gillett 1066 (CAS). Tuolumne Co.: Elizabeth Lake, H. Mason 692 (UC). Johnson Peak, C. Sharsmith 217 (UC). Peak between Matterhorn and Whorl Mts., C. Sharsmith 3826 (UC). Mt. Dana, F. Peirson 7622 (CAS). Trinity Co.: Grizzly Creek, Trinity Alps, E. Carter 1011 (CAS). NV: Elko Co.: Three Lakes, Ruby Mts., A. Borell s.n. (UC). Clover Mts., near Deeth, A. Heller 9242 (US). Ormsby Co.: Fall Creek, C. Baker 1432 (CAS, MICH, RM, UC, US). Washoe Co.: White Creek, E. slope Mt. Rose, P. Train 4420 (UC). Douglas Co.: Mt. Bailey, C. Geddes 18670 (OSC). Klamath Co.:

Crater Lake National Park: Union Peak, *J. Simpson* *9* (UC). Garfield Peak, *W. Baker* *6184* (OSC, UC); *E. Applegate* *9851* (CAS, OSC); *W. Baker* *7203* (WTU). Hillman Peak, *W. Baker* *6401* (UC); *H. Sullen* *s.n.* (OSC). Lane Co.: N. Sister Mt., *M. Peck* *14473* (CAS, OSC). WA: Chelan Co.: Nason Creek valley between Berne and Cascade, *I. Otil* *s.n.* (CAS). Clallam Co.: Mt. Angeles, *J. Flett* *3325* (US). Jefferson Co.: Marmot Pass, Olympic National Forest, *J. Thompson* *9907* (WTU).

A. spathulata

U.S.A.: CA: Del Norte Co.: Douglas Park, on Smith River, J. Thompson (CAS, NY). Smith River Canyon, 15 mi. E. Crescent City, Ripley and Barneby 6798 (NY). Gasquet, A. Eastwood 2211 (NY, US). French Hill, 2 mi. S. Gasquet, J. Tracy 11461 (UC). Smith River at 18 mi. Creek, 3 mi. E. Gasquet, J. Tracy 12284 (UC). Old Gasquet Toll Road, J. Tracy 11208 (UC). State Line, N. Monumental, J. Tracy 19423 (UC). Hayne's Flat Rd. on Coon Mt., J. Tracy 18921 (UC). Grade From Patrick Creek to Shelly Creek, A. Eastwood and J. Howell 3667 (CAS). Gasquet, M. Peacock s.n. (CAS). French Hill, A. Eastwood 2211 (CAS). Patrick Creek, A. Eastwood 12120 (CAS). Gasquet Mt., A. Eastwood 12155 (CAS). Along Hwy 99, 3.2 mi. N. Gasquet, D. Breedlove 3146 (CAS). Gasquet, Parks and Tracy 11208 (US). French Hill, S.J. Wolf 458 (ALTA). 10 km. N. Gasquet, S.J. Wolf 459 (ALTA). 5.8 km N.W. Patrick, S.J. Wolf 387 (ALTA). Siskiyou Co.: Humbug Mt. G. Butler 985 (UC). Raspberry Lake, D. Kildale 8706 (CAS). OR: Curry Co.: 13 mi. S.E. Port Orford, M. Peck 8933 (GH, OSC). Agness, M. Peck 2794 (OSC). Iron Mt., W. Baker 5677 (UC). Snow Camp, J. Thompson 31 (CAS). Douglas Co.: Glendale, T. Howell s.n. (CAN, NDG, US). Jackson Co.: Wimer, E. Hammond 230 (US). Josephine Co.: Caves City, L. Rose 34218 (CAS, MICH, UC). 2 mi. S. Union Mt. Lookout, 12 mi. W. Waters Creek, C.L. Hitchcock and J. Martin 5125 (CAS, UC, WTU). Oregon Mt., A. Kruckeberg 1871 (UC), A. Sweetser s.n. (UC). Kerby,

L.F. Henderson (OSC, UC). Grants Pass, T. Howell s.n. (MICH, OSC). Rough and Ready Creek, E. Meola 99 (OSC). Hwy 99, 1 mi. N. Cave Jct., K. Chambers 2912 (CAS, OSC). Hellgate, Rogue River, M. Peck 8933 (OSC). Wonder Post Office, M. Peck 23777 (OSC). 12 mi. W. Waldo, M. Peck 2916 (OSC). Merlin, L. Smith s.n. (CAS). Finch Ranch, near Kirby, L.F. Henderson 5900 (CAS). 2 mi. S. Wolfcreek, Ripley and Barneby 9552 (CAS, NY). Waldo Jct., D. Kildale 9623 (CAS). Selma, N. Gale 14 (CAS), H. and S. Parks 5947 (UC). Grants Pass, T. Howell 131 (US), C. Piper s.n. (US), Hammond 250 (NY). Caves Jct., near Kirby, L. Rose 34218 (NY). 10 mi. S. Waldo, J. Tracy 4617 (CAS). 17 km. N. Patrick, S.J. Wolf 460 (ALTA). 20 km. N. Patrick, S.J. Wolf 461 (ALTA). Hugo, S.J. Wolf 455 (ALTA). Merlin, S.J. Wolf 456 (ALTA). Store Gulch Guard Station, S.J. Wolf 462 (ALTA). Babyfoot Lake, S.J. Wolf 384 (ALTA).

All known Collections of *A. venosa*

U.S.A.: CA: Shasta Co.: Salt Creek, *Hall and Babcock* *4013* (GH, NY, RM, UC, US). Castella, *L.E. Smith* *348* (CAS). Iron Mt., *L.E. Smith* *s.n.* (CAS, UC). Road to Shasta Bally, 2.2 km S Brandy Creek, S Whiskeytown Lake, *G. Straley* *1791* (UBC), *S.J. Wolf* *469* (ALTA). Bluff above mining road, E of town of Iron Mt., *W. Barker* *227* (WTU). Lamoine Quad: Baker Pine Plantation, W of I-5, T36N, R5W, sec 2, *S. Horner* *112* (STNF), *G. Straley* *1793* (UBC), *S.J. Wolf* *468* (ALTA). Pollard Gulch, T36N, R5W, sec 10 (STNF). Delta Point Rd., below lookout, T36N, R5W, sec 26 (STNF). Backbone Ridge on Lakeshore Rd., T35N, R5W, sec 32 (STNF). Fedners Ferry Rd., T36N, RrW, secs 25, 36 (STNF). Shell Mtn. Quad: 0.5 mi inside National Forest Boundary, Trinity Mt. Rd., T34N, R7W, sec 10, *B. Williams* *251* (STNF). W of Dog Creek Rd. between Tollhouse and Grouse Springs, 7 mi W Delta, E35N, R6W, sec 3, *B. Williams* *369*, *370*, *371* (STNF), *M. Taylor* *3195* (STNF). Head of Stacey Ck., T36N, R6W, sec 34 (STNF). Above forest service rd., 1 mi NW Damnation Peak, T36N, R6W, sec 22, *M. Taylor* *3196* (STNF). McKinsey Ridge, Dog Ck. Rd., T36N, R6W, sec 35 (STNF). French Gulch Quad: South Fork Mt. Lookout to Iron Mt., T32N, R6W, secs 2 and 3; T33N, R6W, sec 34 (STNF). S.W. Whiskeytown Lake, E32N, R6W, sec 20 (STNF). W of Shasta Dam, T33N, R6W, sec 2 (STNF). Dunsmuir Quad: Sims Lookout Rd., T37N, R4W, secs 28, 29 (STNF). Redding Quad: W of Shasta Dam, T33N, R6W, secs 7, 12, 13, 18 (STNF). NW Copeley Mt., T33N,

R6W, sec 24 (STNF). Bollibokka Quad: N.W. Mosoni Mt., T36N, R3W, sec 26 (STNF). Trinity Co.: Schell Mt. Quad: N and N.E. of Jackass Peak, T36N, R7W, secs 14, 24 (STNF). Swift Creek Rd., 0.7 mi. W. Hwy 3, W. of Trinity Center, E36N, R7W, sec 18, B. Williams 363 (STNF).

All known Collections of *A. viscosa*

U.S.A.: CA: Siskiyou Co.: Mt. Shasta, *A. Eastwood 2055* (CAS, GH, UC); *W.B. Cooke 9228* (UC); *W.L. Jepson s.n.* (ND); *R. Bohmannson s.n.* (CAS). Horse Camp, Mt. Shasta, *J.D. Hooker and A. Gray s.n.* (GH); *W.B. Cooke s.n.* (UC), *11501* (CAS, DS, GH, OSC, UC), *13833* (CAS, DS, ND, NY, OSC, UC), *17828* (CAS, WTU); *P. Kamb 1488* (UC); *W.L. Jepson 59i* (JEPS), *W. Dress 3735* (UC); *A.A. Heller 13519* (CAS, DS, NY US, WTU); *W. Barker 232* (WTU); *G. Straley 1411* (UBC); *S.J. Wolf 391* (ALTA). S. slope above ski lodge, Mt. Shasta, *R. Thorne and F. Oettinger 39010* (NY, RSA, UC). Near Wagon Camp, Mt. Shasta, *M. De'Evelyn s.n.* (CAS). Between Panther Meadow and ski lift, Mt. Shasta, *P. Hutchinson 938* (JEPS, K, US). South Gate, Mt. Shasta, *W.B. Cooke 25603* (GH, NY, WTU). Medicine Mt., 41° 33' 48, 121° 36' 30", *G.L. Clifton s.n.* (PUA). Devils Punchbowl, 41° 48' 24", 123° 40' 36", *D.V. Hemphill s.n.* (PUA). Preston Peak, *C.A. Ground s.n.* (PUA). Upper English Lake, 41° 24' 36.2", 123° 12' 53", *F.W. Oettinger 668* (HSC, PUA, UC). Cliff Lake, *G. Muth s.n.* (PUA). Avalanch Gulch, 41° 22' 10", 122° 13' 39", *W.B. Cooke 2000* (UC). Trinity Co.: Trinity Alps: Boulder Creek, *W.J. Ferlatte 1286* (HSC, NY, UC); *W.J. Ferlatte 484* (HSC). Mirror Lake, *J.P. Smith 2361* (HSC).

OR: Deschutes Co.: Three Sisters area, Moraine Lake, E. Rock Mesa and S. of South Sister, *G. Van Vechten 219* (GH, OSC).

Klamath Co.: Crater Lake National Park: Union Peak, J. Mees s.n. (CLNP), F. Colville 1420 (RM, UC); E. Applegate 10090 (CLNP). Hillman Peak, E. Applegate 10126 (CLNP), 10134 (CAS). Shore under Watchman Peak, E. Applegate 9218 (CAS, CLNP). Wizard Island, A.A. Heller s.n. (CAS), 13820 (US). Garfield Peak, W. Baker 7201 (NY, WTU); G. Straley 1946 (UBC); S.J. Wolf 511 (ALTA).

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